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OF THE

MUSEUM OF COMPARATIVE ZOOLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE

VOL. 112

CAMBRIDGE, MASS., U. S. A.
1954 - 1955

The Cosmos Press, Inc.
Cambridge, Mass., U. S. A

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Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 112, No. 1

THE ANT GENUS STRUMIGENYS FRED. SMITH IN THE ETHIOPIAN AND MALAGASY REGIONS

By

WILLIAM L. BROWN, JR.

Museum of Comparative Zoology, Harvard University

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

August, 1954

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 112.

Breviora (octavo) 1952 — No. 35 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 33 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 17 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

These publications issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38 Massachusetts.

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No. 1. — *The Ant Genus Strumigenys Fred. Smith in the Ethiopian and Malagasy Regions*

By William L. Brown, Jr.

This is a part of my revision of the dacetine ant genus *Strumigenys* Fred. Smith, planned to include the entire *Strumigenys* world fauna. For information concerning the characters and relationships of *Strumigenys*, the reader should consult my recent general references on tribe Dacetini (Brown, 1948, 1953). The 1953 reference also contains a detailed discussion of the standard measurements most useful in dacetine studies and the indices derived from these measurements. To recapitulate briefly: TL or "total length" is the sum of the exposed lengths of the head with mandibles, alitrunk, petiole, postpetiole and gaster. HL is the maximum measurable length of the head proper, seen in perfect dorsal full-face view, including all of occipital lobes and clypeus. ML is the exposed length of the closed mandibles from dorsal view (same position from which HL is measured). WL, or Weber's length of alitrunk, is the diagonal distance from base of cervix to metapleural angles, as seen from the side. CI is the cephalic index, or HL/maximum width of head$\times$100. MI, mandibulo-cephalic index, is HL/ML$\times$100. Error of measurement for the head and mandibles should not normally exceed $\pm$0.01 mm.; errors of indices as calculated from raw measurement units should not exceed $\pm$1.

The cooperation of numerous individuals in the entire dacetine project is cited in detail in my 1953 reference, but I should like to acknowledge here the most valuable loans of material and other aid rendered by the following: Dr. George Arnold, of Bulawayo; Prof. Francis Bernard, of the Université d'Alger; Dr. Ch. Ferrière, of the Museum d'Histoire Naturelle, Geneva; Prof. Guido Grandi, of the University of Bologna; Prof. Ed. Handschin, of the Naturhistorisches Museum of Basel; Dr. Harlow B. Mills, of the Illinois Natural History Survey; Dr. E. S. Ross, of the California Academy of Sciences; Dr. George Salt, of Cambridge University; and Dr. Neal A. Weber, of Swarthmore College, Pennsylvania.

Aside from a handful of obscure species in *Microdaceton* Santschi, *Smithistruma* Brown, *Miccostruma* Brown, *Codiomyrmex* Wheeler, and perhaps one or two other small genera at present

known from North Africa, the Ethiopian-Malagasy daeetines fall into two distinet, relatively common, and presumably dominant genera: *Strumigenys* and *Serrastruma* Brown. *Serrastruma* underwent drastic preliminary revision in a reeent paper (Brown, 1952), and it now appears that the number of speeies may have to be redueed still further by synonymy, sinee only four to six of those names appear to represent distinet entities. These few *Serrastruma* species are all very mueh alike, and all are exceptionally variable in a tribe which is otherwise outstanding in the constaney of speeies characteristies. *Serrastruma* appears to be a relatively reeently evolved group of Ethiopian origin; its ancestors are probably to be looked for in *Smithistruma* speeies like those of the *alberti* group. *Serrastruma* is easily the commonest, and apparently the dominating African daeetine genus, and it seems likely (on the assumption that it competes for the same food as other daeetines, namely eollembola and a few other small eryptobiotic arthropods) that its presence is the chief eause of the scareity of other daeetine groups below the Sahara.

The other genus fairly well developed in Africa is *Strumigenys,* which survives as fourteen known, valid species in the Ethiopian Region, plus one in Madagasear. Two of the Ethiopian speeies have become established as tramps outside Africa-Madagascar (*rogeri* and *scotti*), and these will be diseussed below. All of the Afriean *Strumigenys* species elearly belong to one aneestral stock, of which the most generalized known speeies is *S. grandidieri* of Madagasear, although the elose interrelationship of these speeies is masked by extensive morphologieal radiation and might not therefore be guessed at without one's having the complete series of forms in intergrading array. Undoubtedly, other speeies from these regions remain undeseribed and uneolleeted, but in spite of the ineompleteness of the record, it seems elear that the Afro-Madagascan *Strumigenys* fauna is a very limited one compared to the two other distinct faunas of the genus. The New World and Indo-Australian faunas share, roughly equally, at least 100 deseribed and undescribed species that I have been able to verify to date, leaving out those that are clearly synonyms.

The reason for the paueity of the African *Strumigenys* fauna

is not entirely clear, especially in the absence of detailed ecological data, but it seems probable that competition between *Strumigenys* and *Serrastruma* is at least partly responsible. In the other tropical dacetine faunas, *Strumigenys* is usually clearly the dominant genus, though *Smithistruma* is abundant in some of these regions and competes for much the same food (chiefly or entirely collembola of entomobryoid and isotomoid affinities). *Strumigenys* and *Smithistruma* differ, however, in the basic form of the mandibles, and to a certain extent also in details of predatory behavior (Wilson, 1954; Brown, 1954; unpublished data of both authors), so that competition between the two groups is probably only partial. On the basis of evidence I have given elsewhere (especially in the 1953 reference), it seems very likely that the long-mandibulate life-form (*Strumigenys*) is ancestral to the short-mandibulate, or smithistrumiform type. The long-mandibulate type is better fitted for foraging in the open, while the short-mandibulate forms are more suited to cryptic hunting; the former tends to concentrate more toward the tropics, while the latter is predominant, in the Northern Hemisphere, at least, in the warm temperate belts.

In Africa, however, the chief short-mandibulate genus is *Serrastruma,* which exists successfully through most of the continent from South Africa to the Sahara, avoiding only extreme montane and desert habitats. The *Serrastruma* mandibles, a modified and somewhat elongate version of those of *Smithistruma,* may be a very efficient prey-catching instrument, but there is probably more than this behind the success of *Serrastruma.* Probably ecological tolerances and fertility are involved strongly here, as suggested by the extreme morphological variability of the species and the rather larger-than-average nest populations, of which accurate estimates are just beginning to come in.

As mentioned already, the Afro-Madagascan *Strumigenys* so far described all belong to a single group (the *rogeri* group, here so named) representing a common stock. This group, excepting the two probably historically-migrant tramp species, is restricted to Africa and Madagascar, and its relationships with groups of other faunas are not particularly close. With the single exception of *S. rufobrunea,* a widespread and very variable species, the African *Strumigenys* show the narrow ranges of intraspecific

variation usually expected of members of the genus, and ecological specialization, so far as known, follows morphological variation. *Strumigenys* in Africa, as elsewhere, seems to tend to fill the available niches by speciating to specialized types, which then stabilize and become relatively constant and therefore are easily separable one from another. *Serrastruma*, on the other hand, fills many or all of the same niches by producing only a few, but very plastic species.

It is interesting to note that the three truly widespread tramp dacetines [*Strumigenys rogeri* Emery, *Trichoscapa membranifera* Emery and *Quadristruma emmae* (Emery)] are all either certainly or very likely of African origin. In fact, *Quadristruma emmae*, though not yet recorded from Africa proper, is now seen, through the discovery of the intergradient *Strumigenys tetraphanes* (*q.v. infra*), to be a direct offshoot of the *S. rogeri* group and hardly separable from that group except by the detail of the loss of the two smallest antennal segments. In a similar way, *Trichoscapa membranifera* seems close to certain old African stocks of short-mandibulate genera (*Smithistruma, Codiomyrmex loveridgei* Brown, *Miccostruma*), and this species is actually known from various humanly-disturbed areas in Egypt and elsewhere in North Africa. *S. rogeri* is widespread in the West Indies, the Pacific, and in the hothouses of the British Isles, and it has long been thought to be a native Neotropical ant, but I can now show that it is African as its morphological relatives are; the West African *S. sulfurea* proves to be its synonym.

The findings in the Dacetini are in agreement, as concerns tramping ability, with the patterns of colonization now emerging for the ants in general. It would seem, despite certain outstanding exceptions to the contrary, and taking into account the chaotic state of the taxonomy of ants, that the worldwide "tramp habitats" in the tropics and subtropics are occupied mainly by species and genera of African origin. The degree to which this is true will only be surely revealed after much difficult basic taxonomic labor, involving the synonymy of many species and varieties described originally on a purely geographical basis. The origins will be made known chiefly by analyzing group relationships, and then searching for the particular species concerned in its presumed native area, for it is frequently true that in its native

range, an ant elsewhere common as a tramp will be diffusely distributed, or even rare. At present writing, this appears to be the case with all the dacetines mentioned above.

The stages of tramping through the agency of human commerce appear to be fairly obvious. The critical step involves the chance transplantation of a continental propagule to a favorable offshore island with a limited native fauna. If such an island is not already "saturated" with competing tramps, the chances greatly favor the establishment of a very dense population there within a relatively short time. With the pressures of normal continental extraspecific competition, predation and parasitism removed or greatly lessened at the new insular habitat, a dense population is virtually inevitable. From an insular colony, small in area by geographic restriction, but dense in structure, and exposed to intensive contacts with commercial transportation, the probability that new propagules will be transported to new colonial sites is enormously increased over what it originally was in the continental distribution. It seems likely that this is the usual pattern of dispersal of potent tramp species among the smaller insects and certain other invertebrates (the notorious and well-studied giant snail, *Achatina fulica*, for instance; Bequaert, 1950). The study of this problem in the ants is a fascinating one, but very difficult due to the present very great proportion of unrecognized synonyms among the tramp species. From the fragmentary information we have at present, the tramp ants of the tropics and subtropics seem, as has already been mentioned, to be predominantly African in origin. Perhaps, as seems very likely in the better-known but restricted case of the dacetines, this apparent predominance of African forms reflects a relatively potent evolutionary situation centering in the Dark Continent. In the case of the dacetines, Africa certainly would appear to have been the chief center of major-group evolution, at least during the more recent geologic past, as well as the present.

The largest and most generalized member of the *rogeri* group is *S. grandidieri* Forel, from Madagascar. This species shows many similarities in general habitus (as well as in details like the median longitudinal cephalic sulcus, the antennal scrobe posteriorly limited near the compound eye, the preocular notch,

the size, and general head shape) to generalized members of the Indo-Australian fauna (*chyzeri* group) and to American species like *S. mandibularis* Fr. Smith and *S. precava* Brown. The closest relationships of *S. grandidieri* are, however, clearly with the African members of the genus. The generalized *rogeri* group characters include well developed preocular notches combined with rather large eyes, fairly long mandibles with the usual pair of apical teeth forming a fork, and two additional preapical teeth, and a rather strikingly depressed posterior part of the mesonotum.

Important tendencies of specialization within the group include, in different lines, reduction of eye size and loss of the preocular notch, reduction of body size, shortening of mandibles and antennae, and reduction even to loss of the more distal of the two preapical teeth. The reduction of the distal preapical tooth is unique among dacetines in that it takes place asymmetrically, with the tooth on the left mandible diminishing more strongly than that on the right. The tooth on the left may even disappear entirely, while that on the right persists in a more or less reduced state in all but one species (*irrorata*). All stages in the reduction of the distal preapical teeth are found among *rogeri* group species, and each stage furnishes a useful species-constant character.

The eye-notch character and the dentitional asymmetry have received scant attention from most authors, especially Santschi, and in consequence these features are frequently not even mentioned in past descriptions. The published figures of African *Strumigenys*, as well as the mensural citations, are also largely untrustworthy. In the matter to follow, I have not tried to correct by specific mention all of the numerous published errors of detail. Instead, there are emphasized below the essential characters, and especially the measurements, of all species studied at first hand. Special attention has been given to the construction of the key. Type material of all species treated has been directly examined unless otherwise specifically mentioned.

The species included here that were described prior to 1922 have been catalogued (under *Strumigenys s. str.*) in the following references: Emery, 1922, Genera Insectorum, Fasc. 174, pp.

320, 322; Wheeler, 1922, Bull. Amer. Mus. Nat. Hist., 45: 917-918, 1034.

In these lists are included *Strumigenys reticulata* Stitz and *S. ludovici* Forel, both of which have since been transferred to *Serrastruma* (Brown, 1952). *S. reticulata* is a synonym of *Serrastruma lujae* (Forel), while *ludovici* is perhaps a prior name for *Serrastruma alluaudi* (Santschi).

Key to the Species of *Strumigenys* of the Ethiopian and Malagasy Regions, Based on the Worker Caste

Notes on the use of the key. Since most of the species are still known only from scanty material, this key should be taken only as a preliminary guide. Larger series may well reveal that the allowances I have made for potential infraspecific variation, while generous, may in some cases be transgressed. It should also be emphasized that the mere fact that a given specimen does not readily run out in the couplets below is no assurance that the would-be identifier has discovered an undescribed species. It is regrettable that past authors have described in error certain "new" forms solely on the basis that they would not run out in the existing keys. On the other hand, it does seem likely that additional species of *Strumigenys* beyond those here treated occur in Africa.

The identifier using this key must be prepared to measure the dimensions of the head and exposed mandibles to a satisfactory degree of precision. The tolerances of error for these measurements are about ± 0.01 mm. A good-quality manipulator set in a mechanical stage, under magnification of not less than 60 diameters, is recommended for these measurements. It is also advisable to consult a full discussion of dacetine measuring techniques (Brown, 1953).

It goes almost without saying that specimens must be clean and undamaged. Dirt or adhesive lodged in the preocular notches or mandibles can cause serious error, especially at couplets 1, 3 and 10. Furthermore, at couplets 3 and 10 in cases where any doubt occurs, the mandibles should be opened in order to see the dentition properly in at least a portion of any nest series.

At couplet 1, the eye-notches should not be confused with the

antennal scrobes; the latter are broad, usually elongate sulci running for some distance along the sides of the head in such a position as to readily receive the retracted antennae, while the preocular notches run more or less vertically, perpendicular to the long axis of the head, immediately in front of the compound eyes. Specimens should not be mounted flat on the surface of cards; card mounts obscure the details of periocular structure and mandibular dentition, and hence have been the greatest single source of confusion visiting this genus to date. Point mounts, utilizing fine pennant-shaped pieces of card, are by far preferable.

At couplets 3 and 10, the possibility must be considered that rare atavistic specimens may preserve the minute vestige of a left preapical tooth close to the base of the dorsal apical tooth where this (distal) preapical tooth is normally absent in a given species. I have seen one specimen possibly belonging to this category (Bernard ms. new species, couplet 4 and p. 16). Such specimens can usually be detected if a part of a normal series, but uniques will always be difficult, and must be checked by means of dimensions and proportions and other characters given in the descriptions.

1. Ventrolateral border of the head receding sharply at the anterior margin of the eye to form a distinct preocular notch or groove; eye oriented more or less anteriorly and usually more or less detached and narrowly rounded in front.....2
   Ventrolateral border of head not or at most extremely feebly impressed at the anterior margin of the eye; eye oriented entirely laterally, the facets forming a flat or gently convex disc, or the eye reduced to a very few minute facets.....7

2. Larger, length of head proper over 1.0 mm.; each mandible with two short, oblique, truncate preapical teeth (Madagascar) .*grandidieri* Forel
   Smaller, length of head proper under 1.0 mm.; preapical teeth acute...3

3. Left mandible with a single preapical tooth, the distal preapical tooth normally completely lacking (see note above on use of key).....4
   Left mandible with two preapical teeth, the distal tooth smaller than the proximal, but still quite distinct and acute.....5

4. Larger, length of head proper $>$ 0.70 mm.; CI $>$ 72, MI $<$ 54; upper angles of propodeal lamellae low and more or less rounded (Kenya).... .....*londianensis* (Patrizi)

Smaller, length of head proper < 0.60 mm.; CI < 72, MI > 54; upper angles of propodeal lamellae normally dentiform and acute (Congo N. Angola).....new species, Bernard ms.

5. Larger, length of head proper > 0.65 mm.; MI < 42; compound eyes exceptionally large and prominent (Transvaal).....*pretoriae* Arnold
Smaller, length of head proper < 0.65 mm.; MI 42 or more; compound eyes smaller to moderate in size and prominence.....6

6. MI 43-49; mandibular shafts distinctly areuate (W. Africa to Natal and Angola).....*rufobrunea* Santschi
MI 51 or more; mandibular shafts nearly straight (W. Africa; widespread in tropics of both hemispheres, especially in the Pacific and W. Indies; also British greenhouses).....*rogeri* Emery

7. Normally exposed portions of the antennal scapes very broad, less than three times as long as their greatest width; CI about 90 or slightly more (Uganda).....*tetraphanes* new species
Normally exposed portions of antennal scapes more than three times as long as wide; CI well under 90, and usually less than 85.....8

8. Greatest diameter of compound eye distinctly greater than greatest width of antennal scape.....9
Compound eye very small, its greatest diameter less than, or at least not greater than, greatest width of antennal scape.....10
9. Head narrower, CI < 73; mandibles longer, MI > 45 (Seychelles Is.; São Tomé I.).....*scotti* Forel
Head broader, CI > 73; mandibles shorter, MI < 40 (Natal).....
.....*marleyi* Arnold

10. Left mandible with only a single preapical tooth, the distal preapical tooth normally completely lacking.....11
Both mandibles each with two preapical teeth, though in some cases, the distal preapical tooth on one or both sides may be reduced to a minute denticle.....12

11. Right mandible with two preapical teeth, the distal tooth small and normally covered by the dorsal apical tooth of the left mandible at full closure; CI between 70 and 80 (Uganda to Angola)..*dextra* new species
Right mandible with only one preapical tooth, the distal preapical teeth of both mandibles lacking; CI > 80 (Zululand).....*irrorata* Santschi

12. Combined length of head and mandibles when closed > 0.85 mm.; CI < 75; MI 50 or slightly more (Natal).....*havilandi* Forel
Combined length of head and closed mandibles < 0.85 mm.; CI > 75; MI usually under 50.....13

13. Combined length of head and mandibles 0.70 mm. or less; CI *ca.* 81; MI *ca.* 37-38; most hairs on dorsum of head nearly or quite obicular, appearing like round, shining, convex scales or studs (British E. Africa) ..... *stygia* Santschi
Combined length of head and closed mandibles more than 0.70 mm., usually 0.75 mm. or slightly more; CI 77-80±; MI usually > 38; hairs on dorsum of head more or less broadened apically, but not orbicular. 14
14. MI > 43; each humerus with a flagellate hair; HL 0.53 mm. or less. (E. and S. Africa) ..... *tragaordhi* Santschi
MI < 43, usually 41 or less; humeri without flagellate hairs; HL usually greater than 0.53 mm. (E. and S. Africa) ..... *arnoldi* Forel

SYSTEMATIC TREATMENT BY SPECIES

Strumigenys grandidieri Forel

Strumigenys Grandidieri Forel, 1892, Ann. Soc. Ent. Belg., **36:** 517, worker. Type locality: Andrangoloaka Forest, Madagascar. Syntypes: Mus. Hist. Nat., Geneva; Mus. Comp. Zool. Harvard University.

Worker. Descriptive notes are based on two very similar syntypes in the Museum of Comparative Zoology, one of which was measured: TL 5.02, HL 1.33, ML 0.69, WL 1.30 mm.; CI 76, MI 52. Because of its size, this species could hardly be confused with any other African-Malagasy *Strumigenys.*

Head massive, deeply and broadly excised behind, with a distinct, narrow median dorsal sulcus running from clypeus to posterior excision. Antennal scrobes ending, or at least becoming extremely indistinct, at about the level of the eyes. Eyes large, but not so large relatively as in *pretoriae*, convex, prospicient; preocular notch broad and deep, involving the dorsolateral cephalic border.

Mandibles broad, robust, slightly depressed, inserted close together and slightly diverging at full closure. Apical fork of two stout acute subequal teeth, without intercalary tooth or denticle. Each mandible with two short, truncate preapical teeth, directed obliquely anteriorly, subequal in size and scarcely longer than broad, very close to the apex and to each other.

Alitrunk slender, pronotum convex, its anterior margin narrowly rounded and sharply marginate, without humeral angles. Mesonotum reasonably distinct, although the promesonotal suture is obsolescent; posterior mesonotum forming a long slope down

to the strong metanotal groove, from which the nearly plane, platform-like propodeal dorsum rises slightly but rather abruptly; dorsum and declivity of propodeum meeting at approximately a right angle. Propodeal teeth long, spiniform, strongly elevated and divergent; lateral borders of declivity without infradental lamellae, but with three or four fine vertical rugules on each side.

Petiolar node shorter than its slender peduncle, about as broad as long seen from above and narrowly rounded above as seen in lateral view profile; petiolar appendages reduced to insignificant vestiges. Postpetiole transversely elliptical, strongly convex, half again as broad as the petiolar node and less than half as broad as the gaster, with only strongly reduced ventral appendages. Gaster with 9-13 widely spaced, distinct basal costulae extending about 1/5 the length of the basal segment. Gaster otherwise and most of mandibles smooth and shining. Remainder of body, including pleura and both nodes, densely punctulate, opaque. Fine superimposed rugulation on dorsum of head and alitrunk, most distinct on anterior pronotal margin.

Ground pilosity sparse, short, very narrowly spatulate and subappressed on head; available specimens may be partially rubbed. Row of 4 (or 6) longer, suberect, apically very feebly spatulate hairs bordering occipital excision; another pair on vertex. Scape hairs fine, curved apicad; clypeal border hairs narrowly spatulate, curved mesad. A pair of long, erect, very weakly clavate hairs on postpetiole, and a few on posterior half of gaster. Color light ferruginous (possibly somewhat faded); mandibles and head lighter and more yellowish; vertex transversely, nodes and gaster slightly darker than the rest.

Female and male unknown to me.

As already mentioned in my introductory remarks, *S. grandidieri* appears to be the most generalized and most primitive member of the *rogeri* group. Furthermore, it has a "primitive look" backed by size, head structure, form of alitrunk and propodeal armament having much in common with presumed primitive forms of other faunal groups. The species remains known only from the Madagascan type collection, and is the only species of the genus so far recorded from Madagascar proper.

Strumigenys londianensis (Patrizi)

Proscopomyrmex londianensis Patrizi, 1946, Boll. Ist. Ent. Univ. Bologna, **15:** 295, figs. 1, 2, worker. Type locality: Londiani, Kenya (by tautonymy). Additional orig. loc.: Mau Forest, Kenya. Holotype and paratypes: Ist. Ent. Univ. Bologna; paratypes in Brit. Mus. (Nat. Hist.).

Strumigenys (*Proscopomyrmex*) *londianensis,* Arnold, 1948, Occas. Pap. Nat. Mus. S. Rhodesia, **2** (14): 227.

Proscopomyrmex? londianensis, Brown, 1948, Trans. Amer. Ent. Soc., **74:** 128.

Strumigenys londianensis, Brown, 1949, Mushi, **20:** 15.

Worker. Notes based on a single paratype from Londiani, by courtesy of Prof. Grandi. TL 4.2, HL 0.88, ML 0.45, WL 0.88 mm.; CI 75, MI 51. Patrizi gave a short description and large, detailed figures in dorsal and lateral views. In addition to marked contradictions involving dimensions and proportions between the description and figures, and between these and the paratype before me, I note the following:

1. In the paratype, the mandibles are shorter and heavier than as figured, not so strongly arcuate, and the teeth shorter and thicker and set more nearly at a right angle to the shafts. On the right mandible, a short distal preapical tooth is present, but is small and partly covered by the dorsal apical tooth of the left mandible at full closure. The left mandible lacks a distal preapical tooth, but the proximal preapical tooth is well developed on both mandibles.

2. In the paratype, the compound eyes are rounded anteriorly as seen from above, and are not pointed; from lateral view, the eyes appear roughly circular. In front of the eyes is a well-marked vertical groove, extending even into the dorsolateral cephalic borders above and well across the postbuccal surface below. Greatest diameter of eye (*ca.* 0.07 mm.) greater than maximum width of scape (*ca.* 0.05 mm.).

3. In the paratype, the posterior descending mesonotal slope is gently and evenly concave, not interrupted by a suture-like impression as shown in Patrizi's figure 2.

4. In the same figure, the propodeal lamella is much too abruptly terminated ventrally, as is clear even without reference to a specimen. In the paratype, the dorsal angle of the lamella

is lower and more blunt than as shown in the figure, and the excision between upper and lower angles is concavely rounded, not subangular.

5. In the paratype, numerous short, spaced basal costulae meet the anterior border of the first gastric segment. Also, the petiole of the paratype bears feeble vestiges of posterolateral spongiform appendages left out in the figure, and there are small, inconspicuous, reclinate-spatulate hairs on the dorsum of the head of the paratype. The postpetiolar disc is smooth and shining, but dirty.

This species is closely related to *S. rufobrunea* and *Strumigenys* new species of Bernard ms., but is larger than either of these and differs in numerous details, especially the very different propodeal lamellae. It is a forest species still known only from the two original Kenyan collections.

Strumigenys pretoriae Arnold

Strumigenys (*Proscopomyrmex*) *pretoriae* Arnold, 1949, Occas. Pap. Nat. Mus. S. Rhodesia, **2** (15): 267, fig. 8, worker. Type locality: Pretoria, Transvaal. Holotype: Nat. Mus. S. Rhodesia, Bulawayo; paratype in Agric. Res. Inst., Univ. Pretoria.

Worker. Notes based on the single paratype worker, sent through the courtesy of Prof. J. C. Faure for my study. TL 2.8, HL 0.73, ML 0.29, WL 0.70 mm.; CI 73, MI 39. Mandibles stout, gently arcuate, with dentition as in Figure 1a. Eyes exceptionally large and convex, narrowly rounded anteriorly and separated here from the head by a deep, narrow preocular notch as shown in Figure 1b. Posterior mesonotum depressed below level of propodeal dorsum; propodeal lamella with a short but acute, elevated tooth above, convex below (Figure 1c). Petiole with a long, narrow peduncle having a spongiform border beneath; node broader than long, with moderate posterior spongiform fringe. Postpetiolar node transverse, smooth and shining at least in the middle. Basigastric costulae distinct, fanning from bilateral sources and extending almost to the midlength of the basal segment. Head and promesonotum with moderately abundant small, reclinate spoon-shaped hairs; gastric dorsum with sparse erect remiform hairs in transverse rows. Color light ferruginous.

The very large eyes mark this form at once among the Old World *Strumigenys*, and rival those of the Amazonian *S. toeocae* Wheeler. E. K. Hartwig collected the types while "beating for thrips," so it is possible that, like *S. toeocae*, the eye development may be correlated with strongly epigaeic foraging habits, or perhaps even a subarboreal mode of life. Such a correlation holds well for a number of neotropical dacetine ants.

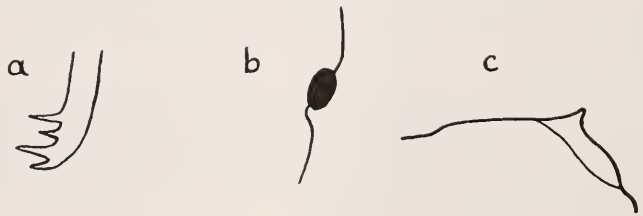

Figure 1. *Strumigenys pretoriae* Arnold, paratype worker; *a*, apex of mandible; *b*, eye and periocular region, dorsal view; *c*, outline of propodeum, lateral view; all to same scale.

STRUMIGENYS new species, Bernard ms.

Worker. Notes based on two workers collected at different localities in the Belgian Congo by N. A. Weber (see below). This distinctive little species is widespread in the Congo drainage system and is apparently common in the southern part of this region, as shown by several small series loaned by Prof. Bernard from the Machado Angolan collections. Prof. Bernard has indicated a desire to describe this species from his more abundant material in his forthcoming work on the Angola ant fauna.

TL 1.9-2.0, HL 0.52, ML 0.29-0.31, WL 0.44-0.45 mm.; CI 69-70, MI 57-60. This very slender species has long, narrow, gently arcuate mandibles and small compound eyes with deep, narrow preocular notches, marking its close relationship to *rogeri*, *rufobrunea* and *londianensis*. The apical teeth are long and slender, longer than in *rogeri* and *rufobrunea*, and the proximal preapical teeth of both mandibles are also quite well developed. In the case of the distal preapical tooth, however, only that of the right mandible is normally present, and even this is difficult to see at full closure because it is then covered by the dorsal apical tooth of the left mandible. In one of the

specimens I have seen, the left mandible bears an extremely minute projection at the proximal side of the base of the dorsal apical tooth, and this projection may be an artifact, a structural defect, or the vestige of a distal preapical tooth. I do not think it wise to mount this specimen for examination by transmitted light until further material is available, as this is one of only two taken by Dr. Weber and deposited in American museums. In any case, the projection is so very small as to be insignificant, and it was not present in any of the remaining samples I have examined.

Localities for material examined: BELGIAN CONGO: 10 miles E. Stanleyville, 1 worker (Weber, No. 2225). Beni to Irumu, Ituri Forest, 1 worker (Weber, No. 2129B). ANGOLA: Collections by A. de Barros Machado, all from vegetable debris of the soil in gallery forest of various river tributaries of the Congo system; Nos. 54-5, 1130-29, 1195-24, forest of Luachimo R., near Dundo; No. 408-1, forest of R. Sanga, branch of R. Luachimo, near Dundo; No. 403-2, forest of R. Tchimana, branch of R. Tchikapa; No. 1430-20, left bank of R. Kasai, NE corner of Angola.

This form is most like *S. londianensis*, from which it differs very markedly in size, form of propodeal lamellae, and other features.

Strumigenys rufobrunea Santschi

Strumigenys rufobrunea Santschi, 1914, Boll Lab. Zool. Portici, **8**: 373, worker, female. Type locality: Conakry, French Guinea, by present selection. Additional orig. loc.: Olokomeji, Nigeria. Lectotype, by present selection, the female from Conakry in Naturhist. Mus., Basel; other original syntypes deposited with lectotype.

Strumigenys (*Proscopomyrmex*) *faurei* Arnold, 1948, Occas. Pap. Nat. Mus. S. Rhodesia, **2** (14): 226, figs. 12, 12a, worker, female. Type locality (orig. designation): Sordwana, Zululand. Other orig. locs.: Richards Bay and St. Lucia Lake, Zululand. Holotype and paratypes: Nat. Mus. S. Rhodesia, Bulawayo. Paratypes: Agric. Res. Inst., Univ. Pretoria; Mus. Comp. Zool. Harvard Univ., etc. NEW SYNONYMY.

Strumigenys petiolata Bernard, 1953 (1952), Mém. Inst. Fr. Afr. Noire, **19** (1): 254, fig. 14 H, I, J, worker. Type locality: Mt. Nimba, French Guinea, 700 M, in termitary in forest. Holotype: Mus. Hist. Nat. Paris. NEW SYNONYMY.

S. rufobrunea is a common and highly variable species ranging widely in tropical Africa. When Santschi first described the species, he overlooked the important eye notches, thus misleading Arnold, who described the same form more accurately under the name *faurei*. The recent description and figures of *S. petiolata* Bernard are in several respects incomplete and self-contradictory, and also fail to show eye notches. I believe this omission is due to the deplorably poor method of card-mounting practiced on ant specimens in many European museums; many of the choice samples sent me from the Old World have been rendered worthless by semi-immersion in adhesive that is virtually impossible to remove in any solvent without damage to pilosity and other important details. One is frequently astonished at the gross inaccuracy of what are supposed to be scientific descriptions, but this astonishment is both explained and magnified anew when the slovenly preparations upon which these descriptions are so coolly based become available for re-examination. It must also be admitted that some American preparations on the more desirable point mounts are so poorly done as to be equally worthless. In my opinion, no descriptive myrmecological work, however pretentious, can be trusted if the material upon which it is based is improperly prepared.

To return to *S. petiolata*: Bernard considered this form closely related to *S. reticulata* Stitz (actually a synonym of *Serrastruma lujae*), to *S. hindenburgi* Forel (an Argentinian species as dissimilar from *petiolata* as its geographical remoteness suggests), and to *S. grandidieri*. Nothing is said about the really closely related forms like *londianensis, rogeri*, and the senior synonyms *rufobrunea* and *faurei*. Though I have not seen the *petiolata* type, and in spite of the confused circumstances surrounding its description, I believe that it is only a fairly large specimen of *rufobrunea* well within the variation outlined below. I have been able to compare directly the type of *S. rufobrunea*, workers and females of the type series of *S. faurei*, and a large amount of other material from diverse localities, and the notes below summarize the specific characters of the two female castes. Special emphasis is placed on variation within the species.

Worker. Measurements are based on 25 workers from at least 11 separate colonies from 8 localities listed below, excepting

the Angola samples. HL 0.50-0.62, ML 0.22-0.30 mm.; CI 75-81, MI 43-49. Examples from single collections: Khor Aba, Anglo-Egyptian Sudan (Weber, 1470), HL 0.62, ML 0.30 mm.; CI 81, MI 48, one worker. Gross Batanga, Cameroon (Sehwab), HL 0.60, ML 0.30 mm.; CI 80, MI 49, one worker. *S. faurei* type series, St. Lucia Lake and Richards Bay, Zululand, HL 0.52-0.56, ML 0.25-0.26 mm.; CI 75-79, MI 45-48, 12 workers. Ituri Forest, Belgian Congo (Weber, 2124, 2129A), HL 0.50-0.51, ML 0.22-0.24 mm.; CI 76, MI 43-47, 4 workers. Haut Mbomu, French Equatorial Africa (Weber, 2187, 2192), HL 0.50, ML 0.24 mm.; CI 76-77, MI 48, two workers. Same locality (Weber, 2188), HL 0.60, ML 0.28 mm.; CI 76, MI 47, one worker. Fort Portal, Uganda (Weber, 2095), HL 0.55, ML 0.25 mm.; CI 76, MI 45, one worker. Although none was measured from the six series collected by Machado in the Congo and Angola (see below), the workers here show a similar range of variation so far as can be determined by simple inspection.

The larger workers often have broader heads and deeper, narrower, more distinct eye notches, but exceptions occur both ways. Larger workers also frequently have the pronotum evenly punctulate, while smaller ones usually have feeble longitudinal rugulation predominating on the pronotum; all intergrades occur. The postpetiolar disc varies from smooth and shining in most series to finely longitudinally striate in the *faurei* types and certain Angolan samples; here again, intergrades are found. The proximal and distal preapical teeth are present on both mandibles, the distal being considerably smaller than the proximal. The shafts of the mandibles are gently but very distinctly arcuate, clearly more strongly so than in *rogeri*. Color varies from light to deep ferruginous, and certain Angolan samples are nearly black.

Female. Lectotype, HL 0.52, ML 0.23 mm.; CI 73, MI 44. A single dealate specimen from Kawanda Experiment Station, near Kampala, Uganda (soil sample under elephant grass, *Pennisetum purpureum* (G. Salt), HL 0.60, ML 0.28 mm.; CI 78, MI 47. Two dealates from *faurei* type series, allonidal, HL 0.57-0.58, ML 0.27-0.28 mm.; CI 80-81, MI 46-47. Total ranges for the above 4 females; HL 0.52-0.60, ML 0.23-0.28 mm.; CI 78-81, MI 44-47. Variation in these and a few Angolan females parallels that of the workers.

Male unknown.

In addition to the localities cited above, six series have arrived after the main work on this species was completed, sent by Prof. Bernard from the collections of Machado, all taken in vegetable detritus in gallery forest in the southern Congo drainage area: BELGIAN CONGO, between Tchikapa and Luluabourg, 100 km. east of Tchikapa. Gallery forests of the rivers Luachimo, Tchimana and Sanga, mostly near Dundo, ANGOLA; Machado Nos. 180-19, 403-2, 408-1, 1195-24, 1210-12, 1248-29.

From the available ecological data, it would seem that *S. rufobrunea* can occupy a great range of habitats, but it appears most often to be found in rainforest or gallery forest, or tree-shaded parts of the savannah. It is the commonest member of the genus in Africa, if collection frequency is any guide. This species could be confused only with *S. rogeri*, but *rogeri* has longer, straighter mandibles and differs in other ways also.

Strumigenys rogeri Emery

Pyramica gundlachi Roger, 1862, Berlin. ent. Zeitschr., **6:** 253, fig. 18a, female, *nec* worker. Type locality: Cuba. Types in Zool. Mus. Univ., Berlin.

Strumigenys rogeri Emery, 1890, Bull. Soc. Ent. Ital., **22:** 68, pl. 7, fig. 6, worker. Type locality: St. Thomas, West Indies. Holotype: Mus. Civ. Stor. Nat., Genoa. Forel, 1893, Trans. Ent. Soc. Lond., p. 378, worker, female, St. Vincent, W.I., biology. Wheeler, 1908, Bull. Amer. Mus. Nat. Hist., **24:** 145, pl. 12, fig. 13, worker, Puerto Rico. 1913, Bull. Mus. Comp. Zool., **54:** 496. Wheeler and Mann, 1914, Bull. Amer. Mus. Nat. Hist., **33:** 40, Haiti. Menozzi and Russo, 1930, Boll. Lab. Zool. Portici, **24:** 163, Moca, Dominican Republic. Santschi, 1931, Rev. Ent., Rio de Janeiro, **1:** 275, Pinar del Rio, Cuba. M. R. Smith, 1936, Jour. Agr. Univ. Puerto Rico, **20:** 856, fig. 12, Puerto Rico, ecology. Donisthorpe, 1915, British Ants, p. 341 (1927, 2nd ed., p. 393), synonymy and refs., summary records from greenhouses in British Isles. Brown, 1948, Trans. Amer. Ent. Soc., **74:** 113, Fiji, Hawaii. Other locality records from West Indies occur in the literature, but are repetitious and will not be cited here.

Strumigenys incisa Godfrey, 1907, Notes R. Bot. Garden Edinburgh, **17:** 102, fig., worker. Type locality: Hothouse, R. Bot. Garden, Edinburgh. Types: locality unknown. Synonymy *teste* Donisthorpe, 1915, *loc. cit.*

Strumigenys sulfurea Santschi, 1915, Ann. Soc. Ent. France, **84:** 261, worker. Type locality: Samkita, Gabon. Syntypes: Naturh. Mus., Basel. NEW SYNONYMY.

Worker. One syntype had an HL of 0.57 mm.; CI 72, MI 53. Ten workers from various West Indian and Hawaiian localities: HL 0.58-0.62 mm., ML 0.30-0.34 mm.; CI 70-74, MI 55. Except for the very slightly smaller size, the syntype agrees very well with abundant material available to me from the West Indies and various Pacific islands. The extra-African material, as would be expected of a tramp species stemming from a single female, or at least from a restricted-locality stock, is unusually uniform. There can be little doubt of the origin of *S. rogeri* in Africa. It has no close relatives in the New World endemic fauna, and it is clearly very close to *S. rufobrunea*, *S. londianensis* and other African species, previous accounts to the contrary nothwithstanding.

S. rogeri is so well known, and so frequently described and figured in the literature, that no new description is required here. To emphasize a few points: the eyes are small, but the preocular notches are distinct, deep and narrow. Mandibles robust, very nearly straight, lying very close together when closed, the preapical teeth two on each mandible, stout and moderate in length, close to apex, the distal tooth much the shorter of the two. Body and head slender; ground pilosity arranged as in related species, inconspicuous. A pair of slender, erect remiform hairs on vertex, a transverse row of four on occiput, one on each side of the mesonotum, and several on the nodes and gastric dorsum; humeral angles each with a contorted flagellate hair. Mesonotum sharply depressed posteriorly, the low portion forming a continuous convexity with the propodeal dorsum. Propodeal lamellae distinct, with short, acute teeth above. Postpetiole more or less smooth and shining. Gastric dorsum with 5 or 6 coarse but not long costulae on each side at base. Color uniform light or yellowish ferruginous.

The female of *S. rogeri* differs from its worker in the usual ways, and the compound eyes are unusually large. It can be distinguished from the *S. rufobrunea* female by means of its slightly narrower head and longer, straighter mandibles, which are a little more than half as long as the head proper. In addition to specimens from most of the localities cited in the synonymy, I have seen material from Micronesia (H. S. Dybas), Jamaica (H. B. Mills), Trinidad (N. A. Weber).

I am fortunate also in having important notes on the biology of *S. rogeri* made by E. O. Wilson during his stay in Cuba in the summer of 1953; these have been turned over to me in their entirety, and I have abstracted them for use here so that the habits of at least one member of the group should be illuminated along with the routine revisionary data. It should be borne in mind that the following notes were made in a habitat other than the native one for the species, and that the majority of feeding notes of this kind necessarily come from observations made in artificial circumstances.

Wilson took his observation colony at San Vicente, Pinar del Rio, Cuba, from a small nest under a rotten limb lying on well shaded ground. The galleries extended into the wood itself. Transferred to a small plaster observation nest, the workers readily captured numbers of entomobryoid collembolans proffered; campodeids up to four times the length of the ants were also always accepted and, like the entomobryoids, were fed to the larvae. Also observed to be chewed by the larvae after capture were a small psocopteran, a small ichneumonid wasp, and a small, injured embiopteran that had previously been ignored by a colony of *Smithistruma nigrescens* Wheeler. A symphylan and a pseudoscorpion, one each, were accepted and eaten by the larvae, but only after lengthy contact with the ants. Other specimens of these last two groups seem to have been refused by the larvae after capture on some occasions. A small polydesmid millipede was also captured, but soon rejected by larvae and workers. Consistently avoided or ignored when offered in the intimate confines of the observation nest were mites, nasute and other termites, small isopods, poduroid collembolans, adult staphylinid and sylvanid beetles of small size, a small campodeiform beetle larva, and dead mosquitoes, though the beetles mentioned disappeared from the nest and may possibly have been eaten. *Drosophila* adults were caught by the adults, but later discarded.

Entomobryoid collembolans seemed to be the usual and preferred prey fed to the larvae, although campodeids were never refused. In feeding habits, therefore, *S. rogeri* follows the generic habit of collembolan predation but, like some other widespread dacetine species, it will also accept a variety of other

small arthropods, particularly campodeids, when available. In hunting, or when disturbed, the workers and females open the mandibles to slightly more than 180°.

In view of the fact that collembolan predation is now known to furnish the basic food supply for widely differing *Strumigenys* species in all three of the major faunas of the world, it seems reasonable to assume that it is general for the genus and also that it is a primitive habit for the genus in the phylogenetic sense. The cases in which the exclusive diet of entomobryoids, isotomoids and symphypleonans is exceeded, show an erratic choice of additional prey, and it does not seem possible at the moment to predict for a given species just what additional kinds of arthropods may be taken over and above the collembolan groups named. This circumstance suggests that widened prey preferences may be secondarily acquired. Relatively common and successful species seem to accept a wider variety of non-collembolan prey than do the ants which are rarer and ecologically more restricted. The rejection of poduroids as prey seems, however, to be nearly or quite universal among *Strumigenys* and the other dacetine genera so far studied. The generality of collembolan predation can probably be extended to all the African-Malagasy species of *Strumigenys*.

Strumigenys scotti Forel

Strumigenys scotti Forel, 1912, Trans. Linn. Soc. Lond., Zool., (2) **15**: 159, worker. Type locality: Mare aus Cochons, *ca.* 1000 ft., Silhouette, Seychelles Is. Syntypes: Mus. Hist. Nat., Geneva.

Worker. One syntype examined through the courtesy of Dr. Ch. Ferrière: TL 2.6, HL 0.67, ML 0.31, WL 0.66 mm.; CI 66, MI 47; scape L 0.40 mm. Twelve workers selected from two large nest series from Makambrera, *ca.* 1300 M., São Tomé Island (B. Malkin): HL 0.59-0.63, ML 0.30-0.32 mm.; CI 68-71, MI 49-51.

The differences in size and proportions between the two samples available are not excessive when one considers that the first is limited to a single example; furthermore, the localities, one on an island in the Gulf of Guinea and the other in the Indian Ocean, are probably secondary ones populated within recent times from the African mainland. As in the case of

S. rogeri, such insular populations are at once more limited in their variability and denser in their structure than the hypothetical parent continental stock, the latter remaining uncollected to the present day. Though I was not able to compare directly the syntype of *S. scotti* with the São Tomé sample because the latter arrived after the type had been returned to Switzerland, my extensive notes on the type reveal no significant differences of the sort that usually distinguish species in this group. In this case offshore colonization may well have proceeded from two different segments of the mainland population.

S. scotti is a medium-sized species without preocular notches. It is similar to *S. havilandi* in general size and appearance, but differs in a number of details, the most readily apparent being the much larger eyes in *scotti*, especially as compared to the more slender antennal scapes (see key). The mandibles are incurved at their bases and have well developed distal and proximal preapical teeth, though the distals are shorter than the proximals. Posterior mesonotum depressed, continuous with plane or feebly convex propodeal dorsum except for a feebly marked metanotal groove. Propodeal teeth sharp, strongly elevated, with narrow, concave lamellae beneath.

Petiole with a rather long peduncle having a narrow ventral spongiform strip; posterior appendages of node nearly obsolete. Postpetiole transverse-elliptical, convex above, smooth and shining, its ventral spongiform appendages moderate in bulk. Basigastric costulae short, indistinct, grouped bilaterally. Ground pilosity of head composed of inconspicuous narrow spatulate reclinate hairs, generally distributed except for the occipital 2/5, where they are much reduced and partly replaced by 6 slender, erect, blunt or subclavate specialized hairs, of which there are also a pair on the mesonotum, a smaller pair on the posterior mesonotum, and groups becoming more numerous on the nodes and gaster. Humeri each with a long, finely flagelliform hair.

A female from one of the Makambrera colonies: HL 0.61, ML 0.31, forewing L 2.3 mm.; CI 72, MI 50. Eyes very large.

Strumigenys marleyi Arnold

Strumigenys havilandi race *marleyi* Arnold, 1914, Proc. Rhodesia Sci. Assoc., **13**: 31, pl., fig. 10, worker. Type locality: Durban, Natal. Syntypes:

Nat. Mus. S. Rhodesia, Bulawayo. 1917, Ann. S. Afr. Mus., **14:** 378, worker.

Strumigenys marleyi Arnold, 1926, Ann. S. Afr. Mus., **23:** 286, worker.

Worker. Two syntypes, TL 2.4-2.5, HL 0.62, ML 0.22, WL 0.60 mm.; CI 76-77, MI 35-36. Related to *S. scotti*, but mandibles much shorter and more broadened at the base, recalling, in less extreme version, certain species of the *Labidogenys* complex of the Indo-Australian Region (*S. biroi* Emery, *S. emdeni* Forel); the trend is surely a convergent one. Distal preapical teeth much smaller than the proximals, the right slightly larger than the left. Apical fork with ventral tooth slightly shorter than dorsal and bearing on its ventral basal surface a small acute adventitious tooth and a minute intermediate denticle. Arnold's figure is highly diagrammatic, and shows a small median clypeal protuberance corresponding to the approximate position of the projecting labral lobes. Eyes weakly convex, with 6-7 facets in the greatest diameter, the diameter being distinctly greater than the maximum width of the scape.

Head and promesonotum covered with small inverted-spoon-shaped hairs, generally distributed dorsally, but no specialized erect hairs. Sparse, short, posteriorly inclined remiform hairs arranged symmetrically on nodes and gastric dorsum.

S. marleyi is known only from the type collection, made by Arnold in a nest of *Pheidole punctulata* Mayr. This *Strumigenys* is similar to *S. scotti* in overall size and form, and in the size of the eyes; on the other side, it seems related by tendencies in the development of mandibles and pilosity to the smaller form, *S. arnoldi*.

Strumigenys havilandi Forel

Strumigenys havilandi Forel, 1905, Mitt. naturh. Mus., Hamburg, **22:** 13, nota, worker. Type locality: "Natal, 5300 feet." Syntypes: Mus. Hist. Nat., Geneva; Natal Mus., Durban; Mus. Comp. Zool. Harvard Univ. Santschi, 1913, Bull. Soc. Ent. France, p. 257, worker, in key. Arnold, 1917, Ann. S. Afr. Mus., **14:** 377, worker

Worker. Two syntypes, TL 2.5-2.8, HL 0.62-0.65, ML 0.33-0.34, WL 0.67-0.70 mm.; CI 71-73, MI 52-53. Mandibles very feebly arcuate, their shafts noticeably tapered apicad; both preapical

teeth of each mandible very slender, long and acute, only a little shorter than dorsal apical tooth. Compound eye minute, scarcely half as wide as the maximum width of the robust antennal scape. Alitrunk in profile very shallowly concave in the posterior mesonotal region, its outline almost straight. Hairs shorter, broader at apices, more numerous and more generally distributed on posterior cephalic dorsum than in *S. scotti*. In addition to the usual sparse erect spatulate hairs, the gastric dorsum bears sparsely distributed short, linear-spatulate appressed hairs. I have not seen the sexual forms of this species, or records other than the original one.

Strumigenys arnoldi Forel

Strumigenys Arnoldi Forel, 1913, Ann. Soc. Ent. Belg., **57:** 114, worker. Type locality: Bulawayo, S. Rhodesia. Syntypes: Nat. Mus. S. Rhodesia, Bulawayo; Mus. Hist. Nat., Geneva?

Strumigenys arnoldi Arnold, 1917, Ann. S. Afr. Mus., **14:** 376, pl. 8, figs. 117, 117 a-d, worker.

I have not seen type material, but have examined a specimen from Pretoria (J. C. Faure), determined by Dr. Arnold, the original collector, and thus presumed authentic. Also available are 3 workers and a dealate female, preserved rather poorly, from Eldoret, Kenya (S. Patrizi). These two samples are closely similar despite the geographical separation. Worker: TL 2.1-2.2, HL 0.54-0.55, ML 0.21-0.22, WL 0.54-0.55 mm.; CI 77-78, MI 38-41. Female: HL 0.60, ML 0.24 mm.; CI 76, MI 39.

S. arnoldi is similar to *S. tragaordhi*, but differs in having a longer, slightly narrower head proper, while its mandibles are both relatively and absolutely shorter. The spoon-shaped pilosity of the anterior cephalic dorsum is broader and more conspicuous, and extends more abundantly to the promesonotum. In these samples of *arnoldi*, the only specialized erect hairs of the alitrunk are one clavate pair astride the mesonotum; no specialized humeral hairs.

Dr. Arnold took the types of this species under a stone in a nest of *Bothroponera krugeri* Forel.

Strumigenys tragaordhi Santschi

Strumigenys Tragaordhi Santschi, 1913, Bull. Soc. Ent. France, p. 257, worker, original diagnosis in key.

Strumigenys traegaordhi Santschi, 1914, Medd. Göteborgs Mus. Zool. Afd., **3**: 28, fig. 4, worker. Type locality: Pietermaritzburg, Natal, by present selection. Additional orig. loc.: Sweetwaters, Natal. Syntypes: Naturh. Mus., Basel.

Worker. Two lectotopic syntypes, courtesy of Prof. Ed. Handschin, HL 0.51-0.52, ML 0.23-0.25 mm.; CI 79-80, MI 45-48. This is a rather "average-looking" small *Strumigenys.* Mandibles weakly arcuate, somewhat broader than as shown in Santschi's figure and gently tapered from base toward apex, enclosing a large oval space at full closure. Distal preapical teeth of both mandibles very small, that of the right slightly larger. Ground pilosity of head composed of narrow inverted-spoon-shaped hairs distributed over the entire dorsal surface, but becoming small and inconspicuous on the extreme occiput. Vertex with a pair of slender, curved, erect, remiform hairs, and a transverse row of four of these on the posterior occiput. Exposed scape L 0.29 mm.; funiculus L 0.44 in the larger of the two syntypes.

Alitrunk slender, resembling that of *stygia*, but promesonotum slightly more convex, propodeal dorsum straight in profile. A flagellate hair on each humeral angle; mesonotum straddled by two pairs of erect remiform hairs, and the usual sparse remiform pilosity on nodes and gaster. Postpetiolar disc smooth and shining. Color light ferruginous, head very slightly darker.

Various authors have recorded this species from widely separated East African localities, but the determinations remain unconfirmed.

Strumigenys dextra new species

Holotype worker. TL 1.6, HL 0.41, ML 0.17, WL 0.40 mm.; CI 76, MI 42. In general size and appearance resembling *S. arnoldi* and *S. tragaordhi,* but a little smaller even than the latter. Eyes very small, almost but not quite as wide as the maximum width of the antennal scape, feebly convex and laterospicient, without a preocular notch or groove. Mandibles gently arcuate, gradually and weakly tapered from base toward apex; dorsal apical tooth decidedly longer than ventral apical and proximal preapical; all of these teeth well developed, slender and acute. Distal preapical tooth present on the right mandible only, small, concealed at full closure by the dorsal apical tooth

of the engaged left mandible; no trace of distal preapical tooth on left mandible. Scape (L 0.63 mm.) gently curved at base, feebly and gradually incrassate at midlength; funiculus (L 0.90 mm.; apical segment L. 0.61 mm.) with greatly reduced, indistinct second and third segments.

Alitrunk in profile gently convex above, with a feeble impression in the region of the posterior mesonotum; metanotal groove virtually obsolete. Propodeum with small but acutely triangular teeth, continued below as feebly concave infradental lamellae. Petiole distinctly and robustly pedunculate; node with gently sloping, bicarinulate anterior face, rounded above, its spongiform appendages reduced to cariniform vestiges. Postpetiole convex, smooth and shining above, with fairly well developed ventral appendages. Gastric dorsum smooth, with a few coarse costulae extending over about the basal quarter of the first segment. Dorsum of head, mesonotum, propodeum and petiole coarsely reticulopunctate, opaque. Pronotum rather coarsely longitudinally rugulose, with broad interspaces weakly shining; posterior sides of alitrunk smooth, shining; appendages, including mandibles, finely and superficially sculptured, more or less opaque.

Ground pilosity of head reduced and inconspicuous, except for a triple row of anteriorly curved spoon-shaped hairs along each dorsolateral cephalic margin from frontal lobe to posterior limit of scrobe. A similar single row, curved apicad, on the anterior border of each scape, and a few hairs forming a clypeal fringe. Ground pilosity reduced, scanty and inconspicuous. Specialized erect hairs remiform to claviform: one pair on vertex; a curved row of 4 along occipital border; one pair straddling mesonotum; a pair on each node; about six transverse rows of 4 each on gastric dorsum, smaller toward gastric apex. Legs and gula with fine, short, flattened reclinate pilosity. Color yellowish ferruginous throughout.

Holotype taken with 6 paratype workers in a soil sample under elephant grass (*Pennisetum purpureum*) at Kawanda Experiment Station, 5 miles north of Kampala, Uganda (G. Salt, No. SS 30). In the same and adjacent samples were taken other presumably hypogaeic ant species (*Ponera coeca* Santschi, *Solenopsis?* sp., and *Strumigenys tetraphanes* new species).

Two additional workers, not paratypes, were seen from Busnia, at the Kenya-Uganda boundary (N. A. Weber, No. 2080) and a single worker from Haut Mbomu, Ubangi Shari, French Equatorial Africa (Weber, No. 2177). Combined measurements for the Kawanda and Busnia series, 9 workers, TL 1.5-1.6, HL 0.39-0.43, ML 0.17-0.18, WL 0.38-0.43 mm.; CI 71-76, MI 40-43. Internidal variation only very slight. Busnia series with slightly broader hairs on the lateral cephalic borders than in the type series. In addition, I have belatedly examined four small series from among the material collected by A. de Barros Machado in Angola, all from the vegetable detritus of the soil of gallery forests of various tributaries of the Congo system: Camissombo, 87 km. south of Dundo, 850 M. (rain forest), No. 1419-6. Luachimo Forest, near Dundo, No. 1248-29. R. Sanga, Dundo, No. 408-1. Left bank R. Kasai, NE corner of Angola, No. 1430-20.

This little species, related to *arnoldi* and the other small forms without eye notches, can be distinguished readily by means of the asymmetrical mandibular dentition, the lateralized development of the cephalic ground pilosity, and the proportions and relatively coarse sculpture. It is widely distributed and apparently rather common in central Africa.

Strumigenys stygia Santschi

Strumigenys stygia Santschi, 1913, Bull. Soc. Ent. France, p. 257, worker, original diagnosis in key. 1914, Voy. Alluaud et Jeannel Afr. Or., Hym., **2**: 113, fig. 20, worker. Type locality: Cave A at Shimoni, coastal British E. Africa. Syntypes: Naturh. Mus., Basel.

Worker. Two syntypes, courtesy of Prof. Handschin, HL 0.49-0.50, ML 0.18-0.19 mm.; CI 81, MI 37-38. See key. Mandibles short, stout, feebly arcuate; dorsal apical and proximal preapical teeth long and slender; distal preapical teeth small, that on right larger than the one on the left. Head broad, and set with broadly suborbicular to orbicular, shining, pale whitish, stud-like hairs over its entire dorsal surface. A row of 4 stubby curved suberect hairs along the occipital margin. Promesonotum broad, depressed, with an indistinct median carinula; farther posteriad. mesonotum narrowed and dorsally weakly impressed, forming with propodeal dorsum a gentle convexity, at the summit of

which is the feebly marked metanotal groove. Each side of mesonotum with a stout clavate hair. Postpetiole superficially sculptured, subopaque to opaque.

Antennal scape (exposed L 0.26 mm.) distinctly broadened at about midlength, its greatest width about 0.05 to 0.06 mm.; sharply narrowed just before apex; funiculus L 0.36 mm. Color rather uniform yellowish-ferruginous. This species is known to me only from the type series.

Strumigenys tetraphanes new species

Holotype worker. TL 2.15, HL 0.54, ML 0.19, WL 0.50 mm.; CI 91, MI 36.

Head broad, in general form like that of *Quadristruma eurycera* (Emery) (1897, Term. Füzetek, 20: pl. 14, fig. 17) of New Guinea; dorsum depressed, only feebly convex. Posterior excision rather deep; occipital lobes rounded, produced laterally at greatest breadth of head bluntly and subangularly; anterior to this, the lateral borders converging strongly; preocular laminae feebly converging, almost parallel. Eyes small, only very feebly convex and without preocular notch, situated on ventral scrobe borders at about cephalic midlength. Clypeus much broader than long, obtusely angulate behind, free border broadly rounded, but feebly emarginate and faintly impressed in the center.

Mandibles short, robust, resembling those of *Strumigenys mocsáryi* Emery (*loc. cit.*, fig. 15) in size, form and position at full closure, but not in dentition. Dorsal apical tooth about 0.13 mm. long, very slender, sharp, feebly recurved; ventral apical tooth straight, slender, more than half as long as the dorsal tooth and feebly diverging from it; no intercalary teeth or denticles. The large spiniform preapical tooth, situated a little distad of midlength of mandible, is about ¾ the length of the dorsal apical tooth and similar in shape and feeble recurvature. About midway between apical and preapical teeth is a minute but acute denticle (=distal preapical tooth), between 0.01 and 0.02 mm. long, that of the right mandible slightly larger than that of the left.

Antennal scape 0.27 mm. long, broadly expanded anteriad,

in shape like a naval cocked hat or the space enclosed by a low normal curve and its baseline. The seapal expansion is not so extreme as in *Quadristruma curycera*, but is considerably more so than in *Q. emmae* (Emery) or any species of *Strumigenys* so far described. Maximum breadth of scape about 0.11 mm.; expanded portion feebly convex dorsally. Funiculus 0.34 mm. long, of which the apical segment occupies slightly more than 3/5; basal segment longer than broad, II, III and IV very short, broader than long; IV as long as or slightly longer than II+III.

Alitrunk distinctive in form. Pronotum and anterior mesonotum together forming an almost perfect circle as seen from above, this surface rather strongly depressed dorsally and with blunt, overhanging lateral pronotal margins; humeral angles not developed. The surface of this promesonotal disc is divided by the feeble, sulciform, semi-circular promesonotal suture; pronotum with an anteromedian and bilateral, and the mesonotum with an anterior, dorsal convex area. Behind the promesonotal disc, posterior mesonotum immediately and strongly depressed and narrowed, and as seen from above continued posteriad by propodeum to form with it an oblong, parallel-sided section slightly shorter than the promesonotal disc and less than half as broad; this section as seen from the side forming one continuous, convex dorsal outline, and without lateral margins as seen from above. Metanotal groove visible on dorsum as a darkened line. Propodeal declivity steep; teeth short, half as long as the distance between the centers of their bases and only moderately acute, continued below by feebly concave infradental lamellae which are almost as broad as the height of the teeth.

Petiolar peduncle laterally compressed and longer than its node. Node small, anteroventrally compressed, broader than long; as seen from the side high and narrowly rounded at the dorsal apex. Petiolar appendages reduced to fine vestiges, midventral strip represented only as a low, non-spongiform carina. Postpetiole forming a transverse ellipse, about twice as broad as long and nearly twice as broad as the petiolar node; strongly convex dorsally; appendages fairly well developed, but largely restricted to the venter. Gaster slightly narrower than head, somewhat depressed; anterior spongiform margin medially emarginate.

Gastric costulae coarse, radiating from bilateral origins, about 7 or 8 on each side, those nearest the middle oblique, enclosing a free narrow median triangular area; longest costulae extending nearly 1/3 the length of the long basal tergite; gastric dorsum otherwise appearing very finely and superficially reticulate (perhaps due in part to a film of secretion), but still very strongly shining. Sides of posterior alitrunk shining, but feebly roughened as on the gastric surface. Mandibular teeth shining. Remainder of body densely punctulate, opaque; postpetiole with very feeble superimposed longitudinal rugulosity.

Dorsum of head from about midlength to posterior clypeal border thickly set with conspicuous, heavy, suborbicular, subappressed, inverted-spoon-shaped hairs; a double row of the same extends posteriad along each dorsolateral cephalic border as far as the blunt lateral occipital angles, and a single row of the same, large and very conspicuous (6-7 hairs) lines the anterior border of each scape. Similar, but very much smaller and less conspicuous hairs on the clypeus and posterior half of the cephalic dorsum; contrast between the pilosity of anterior and posterior parts of head quite striking, as in certain other species of the *S. rogeri* group (e.g., *scotti*). Hairs on anterior clypeal border similar to the foregoing, intermediate in size, subappressed, 4 on each side of the middle. Alitrunk with a sparse and altogether insignificant complement of minute appressed hairs, the surface appearing nude except for a prominent pair of short, erect, strongly elavate mesonotal hairs. A pair of the same is directed posteriorly from the postpetiole, and there are about twelve (some possibly broken off) on the gastric dorsum, diminishing in size apicad. Legs and scapes with small appressed spatulate hairs. Underside of head with fine subappressed pubescence; inner borders of mandibles with a few long fine hairs.

Color ferruginous yellow, dorsal surfaces a trifle darker.

Holotype a unique worker taken in a soil sample from under elephant grass at Kawanda Experiment Station, 5 miles north of Kampala, Uganda, on Feb. 15, 1949 (G. Salt) with *Strumigenys dextra* new species (*q.v.*) and other ants. Holotype deposited in Museum of Comparative Zoology, Harvard University.

This aberrant member of the *rogeri* group is of more than

usual interest because it shows affinities to the tropicopolitan tramp species *Quadristruma emmae* (Emery), and in fact nicely links this little form to the *rogeri* group, and thus to genus *Strumigenys*. The fact that *Q. emmae* has only four segments in the antennae still separates it from *Strumigenys*, but the extreme reduction of the second and third funicular segments in *S. tetraphanes* makes this difference largely an academic one. A reappraisal of the genera of subtribe Strumigeniti may well reveal that *Quadristruma* Brown (1949) should be merged with *Strumigenys*, but whatever the eventual decision, it seems plain now that *emmae* is African, not Papuasian, in origin, and that the *rogeri* group is directly ancestral. The other *Quadristruma* species, *Q. eurycera* (Emery), may not belong to the same stock as *emmae*, and its resemblances to *emmae* and *tetraphanes* may well be convergent ones. The final generic review of the Dacetini will see this relationship altered in some manner.

S. tetraphanes is readily separated from the other members of the *rogeri* group by means of its broad head and short mandibles, and above all by means of its very broad antennal scapes.

Strumigenys irrorata Santschi

Strumigenys irrorata Santschi, 1913, Bull. Soc. Ent. France, p. 257, worker, original diagnosis in key. 1914, Medd. Göteborgs Mus. Zool. Afd., **3**: 29, fig. 5, worker. Type locality: Lake Sibayi, Zululand. Holotype: Naturh. Mus., Basel.

I have not been able to view the unique worker type directly, but Prof. Handschin has very kindly sent me pencil sketches in answer to my inquiries. These confirm that both mandibles lack the distal preapical tooth, although both mandibles are shown as having long proximal preapical teeth. The compound eye is portrayed as small, its greatest diameter less than the greatest scape width; the drawing shows no obvious trace of a preocular notch. As measured from Santschi's figure (*loc. cit.*), which may or may not be accurate in showing proportions, the CI would be about 84 and the MI about 41. Santschi gave the length as 1.5 mm. total, which is probably too low.

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Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 112, No. 2

DEEP WATER ELASMOBRANCHS AND CHIMAEROIDS FROM THE NORTHWESTERN ATLANTIC SLOPE

by

Henry B. Bigelow

and

William C. Schroeder

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

September, 1954

No. 2 — *Deep Water Elasmobranchs and Chimaeroids From the Northwestern Atlantic Slope*[1]

By Henry B. Bigelow and William C. Schroeder

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[1] Contribution No. 692 from the Woods Hole Oceanographic Institution.

INTRODUCTION

The slope of the bottom is so steep from the edge of the continent at the 150-200 fathom level down to the 800-900 fathom level off the northeastern United States and off Nova Scotia that the intervening zone is not wider than about 25 miles, anywhere between the offing of Chesapeake Bay and the Laurentian Channel, with a minimum breadth of only 7-10 miles. Nevertheless this zone, narrow though it be, is of great interest ecologically, because it is the site of the transition from the bottom-dwelling animals of the shallow waters of the continental shelf, to those of the Atlantic abyss.

The explorations by the "Blake," and especially those by the "Albatross" in the 1880's, yielded a wide variety of bottom-living fishes from the lower part of the slope at depths of 800 fathoms and more; they also sampled the bathypelagic communities of the overlying waters, many additional members of which have been brought to light subsequently. The fishes, too, of the northeastern American shelf have been studied intensively at many hands for many years, not only from the descriptive-taxonomic standpoint, but also from the standpoint of the commercial fisheries.

But the "Albatross" and "Fish Hawk" devoted less attention to the middle part of the slope. (They made only 63 trawl hauls at 250-500 fathoms, contrasted with 117 hauls deeper than 700 fathoms). And no subsequent attempt has been made to continue the scientific investigation of the bottom-living fishes in deep water in the northwestern Atlantic since 1887 when the "Albatross" was transferred to the Pacific, whether because of the expense that would have been involved, or because of a shift of interest to other subjects. And very little commercial fishing, either with hook and line or with the trawl, has ever been attempted deeper than about 250 fathoms along the slope with which we are concerned, partly because of the difficulty and expense of operating commercial gear in greater depths, and partly because it has not seemed likely that saleable food fishes would be found on bottom there in worthwhile quantities.

Consequently, while it seemed safe to forecast, from the fish faunae of shallow water and of deeper, what species of bottom fishes might be expected along the mid zone of the slope, the

belt in question was a *mare incognitum,* to all intents and purposes, as regards the quantities of any species to be found there.

In the hope of filling this gap in our knowledge, trawling campaigns were carried out by the Woods Hole Oceanographic Institution along the slope between the offings of southern New England and of La Have Bank, Nova Scotia, on the "Caryn" in June and September 1949; between the offings of Montauk, Long Island, New York, and of La Have Bank from the dragger "Cap'n Bill II" in June and July 1952; and between the offings of Virginia and of La Have Bank on "Cap'n Bill II" in June and July 1953. Otter trawls 35 feet wide were used in 1949, 35 and 50 ft. trawls in 1952, and 60 ft. trawls in 1953. One hundred and forty-three successful hauls were made in the three summers combined, dragging on bottom for 30-60 minutes, between 200 fathoms and 730 fathoms. And a total catch of about 25,000 bottom fishes in all the hauls combined seems good evidence that the nets worked with at least moderate efficiency.

The present report deals with the catches of elasmobranchs and of chimaeroids.

The following species of sharks and skates had been reported, through 1953, from depths greater than 200 fathoms on the American Atlantic slope north of Chesapeake Bay: *Apristurus profundorum* Goode and Bean 1895; *Centroscyllium fabricii* (Reinhardt) 1825; *Etmopterus princeps* Collett 1904; *Centroscymnus coelolepis* Bocage and Capello 1864; *Raja bathyphila* Holt and Byrne 1908; *Raja jenseni* Bigelow and Schroeder 1950; *R. mollis* Bigelow and Schroeder, 1950; *R. laevis* Mitchill 1817; *R. senta* Garman 1885; and *R. spinicauda* Jensen 1914. On the other hand, one species — *Scymnodon melas* — described by Bigelow, Schroeder and Springer (1953, p. 233) as new must now be relegated to synonymy (p. 51).

The trawling operations of "Cap'n Bill II" add *R. fyllae* Lütken 1887 to this list. And it is likely that *R. hyperborea* Collett 1878 will be found off Labrador or off Newfoundland sooner or later. But the number of trawl-hauls that have been made along the 300-550 fathom zone between the Hudson Canyon and the offing of La Have Bank, Nova Scotia, is now so large that the list of elasmobranchs to be found on the bottom there is not likely to be increased much in the future.

SHARKS

Family SCYLIORHINIDAE
Cat Sharks

Apristurus profundorum (Goode and Bean) 1895

This deep-water shark had been known from two specimens only, both of them from the offing of Delaware Bay, until the summer of 1952 when "Cap'n Bill II" trawled it at 7 stations (8 specimens) scattered along the slope from the offing of New York (Lat. 39°46′N, Long. 71°35′W) to the offing of southern Nova Scotia (Lat. 42°39′N, Long. 63°54′W). And with 8 more, taken in 1953 at 6 stations, the records for it are numerous enough now and distributed widely enough to show that it is to be found generally, though sparsely, along the slope from the offing of Nova Scotia to that of Virginia (most southerly station, Lat. 37°39′N, Long. 74°06′W; most northerly, Lat. 42°40′N, Long. 63°52′W). The depths of capture range between 360-420 fathoms and 640-720 fathoms for the two years combined. The temperature on bottom, at the stations where it was taken, was 3.7° to 4.5°C in 1953, and presumably was about the same in 1952, though no bottom readings were taken that year at the particular localities in question.

Points of taxonomic interest are discussed in our earlier paper (Bigelow, Schroeder and Springer, 1953, p. 214).

Family SQUALIDAE
Spiny Dogfishes

Centroscyllium fabricii (Reinhardt) 1825
Black Dogfish

Earlier captures of the black dogfish on the slopes of the Nova Scotian Banks, and of Georges Bank, had not been numerous enough to suggest the existence of more than a sparse population there, though a widespread one as had been known for many years. In fact, only two specimens had come into our hands, in the Museum of Comparative Zoology, at the time when our earlier discussion of its occurrence in the western Atlantic was written (Bigelow and Schroeder, 1948a, p. 486). But catches of 69 black dogfishes by "Caryn" in 1949, and of 715 and 371 of them by "Cap'n

Bill II" in 1952 and 1953 respectively, show that our previous estimate of its numbers off Nova Scotia and off Georges Bank must be revised upward. This seems, indeed, to be the most plentiful shark there at depths greater than those frequented by the common spiny dogfish (*Squalus acanthias*).

No doubt the reason for the quantitative discrepancy between the older records for the species in Nova Scotia slope waters, and the catches of it made there in 1949, 1952 and 1953 is that all of the former were based on fish taken with hook and line by the halibut fleet which did not fish much below 200 fathoms, i.e. not deep enough to sample more than the uppermost fringe of the population of this deep-water shark.

The number of specimens at hand is now large enough to throw some light on the quantitative occurrence of the species, both geographic and bathymetric. The average catches, per successful haul,[1] within the depth range where *fabricii* was taken at all, were about 24 specimens to the eastward of longitude 66°W for the years 1949, 1952 and 1953 combined (49 hauls); between 4 and 5 specimens from longitude 66° to longitude 69°59′W (26 hauls); 2 specimens from longitude 70° to longitude 71°59′ (10 hauls); and about 1 specimen westward and southward thence to the offing of Virginia (12 hauls). Similarly, the largest catches made in any one haul were 92 and 95 specimens east of longitude 66°; 29 between longitudes 66° and 69°59′W; 8 between longitudes 70° and 71°59′W; and 3 farther to the west and south. The regularity, too, with which *fabricii* was taken shows a corresponding gradient from northeast to southwest, for while 97 per cent of the hauls made in 1952 and 1953, within its preferred depth zone, yielded it to the eastward of longitude 66°, only 65 per cent did so along the slope off Georges Bank (longitudes 66° to 69°59′); 60 per cent in the offing of southern New England (longitudes 70° to 71°59′); and 50 per cent farther westward and southward.

Evidently, then, the center of abundance for *fabricii,* in American waters, lies at least as far to the eastward and northward as the offing of western Nova Scotia, perhaps farther still in that direction. Even here, however, the black dogfish — like other fishes — vary widely in numbers from place to place within

[1] We take no account of such of the hauls as obviously were unsuccessful for one reason or another.

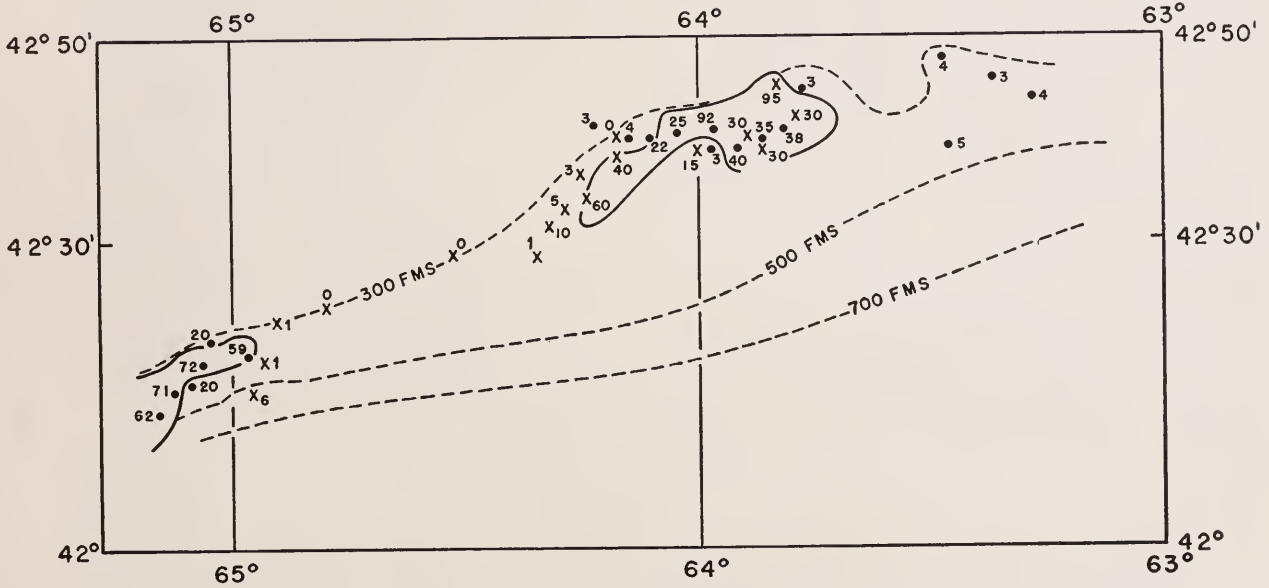

Fig. 1. *Centroscyllium fabricii.* Numbers per haul taken east of longitude 66°W in 1952 (•) and in 1953 (x). The solid curves enclose the areas where the catches per haul were consistently greater than 25.

short distances, independent of the precise depth, as is illustrated by catches ranging from 3 to 92 per haul within a distance of about 5 miles along the 340 to 520 fathom zone between longitudes 63°58′ and 64°06′ in 1952; from 15 to 95 per haul within about 10 miles in that same general region in 310 to 625 fathoms between 63°50′ an 64°00′ in 1953; and from 5 to 40 within a few miles to the southwestward (longitudes 64°10′ to 64°17′; 280 to 475 fathoms) that same summer. But a plot of the catches made per haul (Fig. 1) shows that these were not haphazard, for in each year there was a definite center of abundance, concentrating at about longitudes 63°50′ to 64°10′, extending for something like 30 miles along the slope between 310 and 545 fathoms, with the bottom less productive both to the northeastward and to the southwestward. And a similar concentration was encountered some 35-40 miles to the southwestward (longitude 65° to 65°10′) in 1952 at about that same depth (310-490 fathoms). This precise locality was not revisited in 1953. The discovery of these rather definite centers of population is of general interest as evidence that the relative productivity of the bottom, in fishes, may vary as widely from place to place, far down the slope, as every fisherman knows that it does on the great fishing banks on the continental shelf.

It may be worth adding that an average catch of 21 specimens per haul, with the trawls used, would work out at about 4 specimens per acre, the richest catches (92 and 95 per haul) at about 18 per acre — if the trawls caught all the specimens lying in their path, which they certainly did not; how much to add for failure in this respect would be sheer guesswork.

If the catches can be taken at face value, *fabricii* is only about ⅕-⅙ as numerous along the slope of Georges Bank and off southern New England as it is off Nova Scotia, and still less numerous farther to the west and south.

Nevertheless, captures of five specimens off Delaware Bay in 3 hauls (Lat. 38°41′N-38°47′N), of one off the coast of Maryland (Lat. 38°05′N), and of one off the coast of Virginia (Lat. 37°39′N) show that *fabricii* ranges farther to the southward, along the American Atlantic slope, than had been known previously.

Off Nova Scotia, the shoalest capture of *fabricii* was in a haul at

185-220 fathoms (3 specimens); the largest catches (92 and 95 specimens) were made between 310 and 360 fathoms; and the species seems to have been distributed rather uniformly down to about 600 fathoms, to judge from average catches of about 28 per haul at 301-400 fathoms, of 22 at 401-500 fathoms, and of 33 at 501-600 fathoms. But catches of only 15 in a haul at 610-625 fathoms, and 6 in one made at 660-705 fathoms[1] suggest that *fabricii* is less plentiful deeper than 550 fathoms than shoaler. But average numbers of specimens taken per haul at different depths may be deceptive, if taken by themselves, for they conceal the fact that the numbers caught, in individual hauls, varied about as widely within representative depth zones as they did geographically (Fig. 1), no doubt for the same reason.

Maximum and minimum numbers caught per haul, east of longitude 66°W, in 1949, 1952 and 1953 combined, at depths greater than 300 fathoms, are as follows:

Depth in fathoms	Number of hauls	*Fabricii* caught per haul
301 - 350	12	3 - 95
351 - 400	6	4 - 71
401 - 450	7	0 - 59
451 - 500	6	1 - 40
501 - 550	4	3 - 62
551 - 600	1	5
601 - 650	1	15
651 - 700	1	6

Farther to the west and south *fabricii* is not only less numerous, but the upper boundary to its vertical range lies deeper down the slope, progressively. Thus the shoalest hauls in which it was taken were at 355-400 fathoms (1 specimen) and 360-420 fathoms (2 specimens) along the slope of Georges Bank, at 390-460 fathoms (3 specimens in 3 hauls) in the offing of southern Massachusetts, and 485-520 fathoms, southward from the offing of New York.

[1] These were the only hauls to the eastward of longitude 66° that worked as deep as 600 fathoms, either in 1952 or in 1953.

The deepest catches were made at 660-705 fathoms off Nova Scotia (6 specimens in one haul); at 600-670 fathoms off Georges Bank (5 specimens in 1 haul); at 710-730 fathoms off southern Massachusetts (5 specimens in 1 haul); at 630-675 fathoms (3 specimens in 1 haul) and at 640-720 fathoms (2 specimens in 1 haul) farther to the westward and southward. As these were the deepest successful hauls, with one exception, that were made in the respective sectors of the slope, it is a question for the future how much deeper the range of *fabricii* may extend.

In 1953, when the temperature was taken on bottom with maximum-minimum thermometers at almost all the stations where trawl hauls were made, all the captures of *fabricii* occurred where bottom temperatures ranged between about 4.5°C, and about 3.3°C, the great majority between 4.5° and 3.9°. And even if the range of *fabricii* reaches down as deep, say, as 1200 fathoms — of which there is no evidence — its lower thermal boundary along the American slope would not be colder than about 2.5°C. At the other extreme, specimens that work their way up the Nova Scotian slope to 200 fathoms or so, such as were brought in by the halibut fleet years ago, are likely to meet water at least as warm as 6-7°C. Thus, the range of temperature within which it occurs in greatest numbers in American waters is only about 2°C, the extreme range there perhaps 4-5°C for the entire population.

Consequent on the steepness of the slope, the maximum breadth of the zone where *fabricii* occurs the most regularly is only something like 25-30 miles off the Grand Banks and off Nova Scotia, even if it ranges down to 1000 fathoms there; 10-12 miles along Georges Bank and off southern New England; and perhaps 15 miles in the offing of Maryland and of Virginia.

The catches of *fabricii* made east of longitude 66°W averaged considerably larger in 1952 than in 1953 as tabulated below. But with the catches in individual hauls ranging from 1 to upwards of 90 in each of the two years, the discrepancy may not be wider than can be credited to what we may call "fisherman's luck," for want of a better name.

Catches east of longitude 66°W, at depths greater than 300 fathoms

	Successful hauls	Hauls with *fabricii*	Percentage of hauls with *fabricii*	Total catches	Average per haul	Maximum catch
1952	19	19	100%	610	32	92
1953	15	14	93%	333	22	95

Among 25 specimens that were opened in 1953, 10 were empty; the others contained remains of fishes, decapod crustaceans, (shrimps), schizopod or euphausiid, squids, and octopus.[1]

Etmopterus princeps Collett 1904

We have already reported (with description) the capture of 47 specimens of this deep-water shark along the slope between the offings of southern New England and western Nova Scotia (Bigelow, Schroeder and Springer, 1953, p. 47). Earlier records for *princeps* had been from the Faroes-Hebrides region (Collett, 1904, p. 3; 1905, p. 28) and from the offing of the Straits of Gibraltar (Koefoed, 1927, p. 21). The trawlings of 1953 yielded 7 more, all of them from the offing of western Nova Scotia. The largest numbers taken were 9 (once), 8 (once) and 7 (once) while 1 was the number taken the most often (fourteen times).

The hauls that took *princeps*, in the three seasons, were at depths ranging from 310-320 fathoms down to 490-540 fathoms, with the largest catches (7, 8 and 9) at 480-520 fathoms, 420-480 fathoms, and 390-440 fathoms respectively, which suggests that *princeps* is about equally plentiful, downward, across the depth zone along which it occurs off our coasts. And it is to be expected considerably deeper there as well, for it has been taken at 1134 fathoms off the Straits of Gibraltar.

The 18 hauls that yielded it in 1949 and 1952 were scattered all along from the offing of La Have Bank (longitude 63°38′W) to the offing of Cape Cod (longitude 70°05′W), with the largest catches (3, 7, 8 and 9 individuals) off Nova Scotia. Similarly, 5 of the 7 specimens taken in 1953 were from the general offing of La Have Bank, only 2 off the eastern part of Georges Bank, although many successful hauls were made there and to the

[1] Stomach contents identified by Dr. Benjamin Laevitt.

westward along the 300-550 fathom zone that summer. It is a question for the future whether this difference is evidence of a corresponding fluctuation in the western boundary of *princeps*, in numbers large enough for the trawl to pick it up, or whether we are dealing with a matter of pure chance. In either case, there is nothing to suggest that this shark ranges westward beyond the offing of Cape Cod, a limitation we cannot explain as due to temperature, for readings taken by "Cap'n Bill II" in 1953 on bottom along the 300-550 fathom zone were very nearly the same to the westward of longitude 70°W (3.5°-4.8°) as to the eastward (3.3°-4.5°).

Centroscymnus coelolepis Bocage and Capello 1864
Portuguese shark

The trawlings of 1953 yielded three specimens of this species: two juvenile males, 565 mm. and 690 mm. long, and an adult female of 1035 mm. which gave premature birth on deck to 15 embryos 266-282 mm. long, 5 of them males and 10 females. The number of embryos is in line with Vaillant's (1888, p. 66) record of 13 to 15 for this species. Moreau (1891, p. 9), it is true, has reported only 5 for a Mediterranean female, identified as *coelolepis*, but her small size (599 mm.) suggests that she belonged to some other species in reality.

It has been a tacit assumption, until recently, among students of sharks, that the denticles which develop on any given part of the body at different stages of growth are similar in shape; hence, that the shape of the denticles is a more or less reliable specific character — or even a generic one. But Radcliffe (1916, p. 267) has pointed out that the denticles to be seen on specimens of different ages differ somewhat in shape in some species of the genus *Carcharhinus*. Tortonese, too, (1952, p. 386, fig. 1; p. 387) has recently found that the denticles on the sides of a juvenile male, 270 mm. long, seemingly referable to *Centroscymnus coelolepis* by other characters, were strongly tridentate, whereas those on the adult *coelolepis* have evenly rounded edges, as has been known for many years. And the "Cap'n Bill II" series of that species enables us to corroborate his very interesting finding. Thus those on the body of our adult female 1035 mm. long are

evenly ovoid in outline, with concave crowns, and regularly overlapping (Fig. 2*D*) ; they have been pictured and described similarly for this species by Bocage and Capello (1866, pl. 3, fig. 3), by Vaillant (1888, pp. 64-65), by Garman (1913, pl. 14, fig. 8), and by us (1948a, p. 495, fig. 94A). But the denticles on the embryos to which she gave birth[1] are tridentate, weakly so on the top of the head, where they are moderately widely spaced, but much more strongly tridentate on the sides of the body where they are more widely spaced as well (Fig. 2*A*).

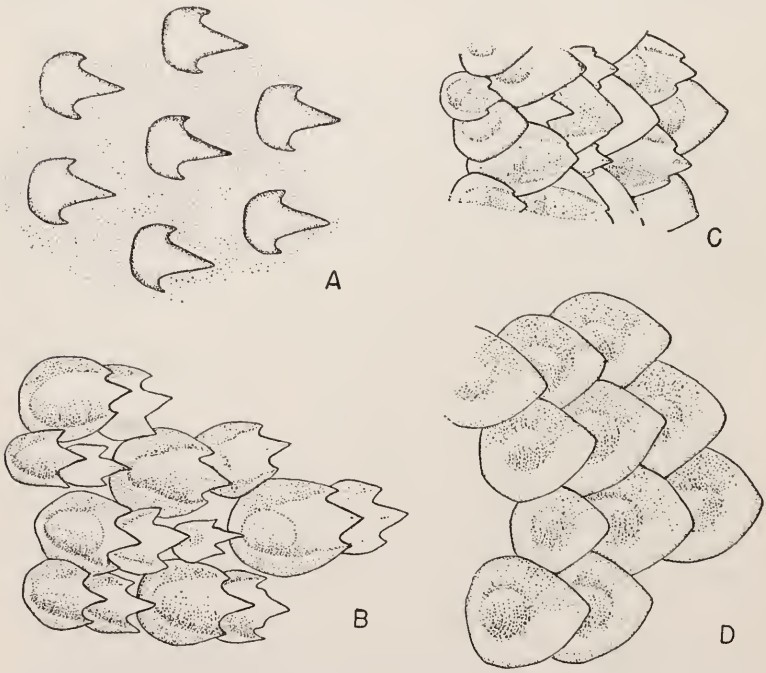

Fig. 2. *Centroscymnus coelolepis.* Dermal denticles from side of trunk below first dorsal fin. *A*, Embryo male, 282 mm. long, from adult female of 1035 mm., about 13 x. *B*, Juvenile male, 565 mm. long, about 8 x. *C*, Juvenile male, 690 mm. long, about 6 x. *D*, Adult female 1035 mm. long (mother of embryo shown in *A*), about 5 x.

[1] Embryos well formed, but with only the tips of the teeth exposed, while the denticles had not yet erupted through the skin.

It is evident, too, from partly grown specimens of different sizes that the margins of the denticles that are developed successively, during growth, are less and less dentate. The smaller of the denticles, for example, on the flanks and belly of a juvenile male 565 mm. long are strongly tridentate still, but the larger (i.e. younger) ones only weakly so, and with one overlapping the next more or less widely in most cases (Fig. 2*B*). At this stage the denticles on the sides below the first dorsal fin range from about 1.2 mm. to about 2 mm. in length.

At a slightly more advanced stage, as represented by a male of 690 mm., the smallest (i.e. the oldest) of the denticles on the trunk are tridentate (Fig. 2*C*), but many of the larger (i.e. younger) ones now have entire margins, though with pointed tips still, while denticles of intermediate sizes show various intermediate stages and the denticles on the body now overlap so regularly that they hide the skin.

Up to this stage the denticles vary considerably in size from one to the next, with those on the sides below the first dorsal fin ranging from about 1 mm. to about 2.4 mm. in length. But those on the adult female of 1035 mm. (Fig. 2*D*) are all about equal in size over any given region of the body. And they no longer include any tridentate forms except near the tips of the pectoral fins.

This seems an appropriate place to remind the reader that on adult *coelolepis* (females, at least; adult males have not been seen) the denticles are largest (about 3-3.5 mm. long) on the mid sector of the trunk, belly as well as sides and back, and are progressively smaller not only forward, but rearward as well, with those on the caudal peduncle on the average only about 70 per cent as long as those on the sides below the first dorsal fin.

The discovery that the denticles are of one shape on young specimens of this particular species of shark, but of a strikingly different shape on adults, opens vistas that are interesting from the standpoint of elasmobranch morphology in general, as well as from that of taxonomy.

To begin with, it poses the question, how long is the normal life span of a dermal denticle in relation to the life of the individual? So far as we can learn, no special attention has been paid to this point, nor is it safe to reach any conclusion *a priori*

here, for while the teeth of sharks, which correspond in all essentials with the placoid scales or dermal denticles, are replaced periodically, the dorsal fin spines — equally homologous with the denticles — are retained throughout life in such sharks as have them. Among bony fishes, the general rule is that a scale, once formed, persists throughout the life of the fish, growing in size meantime, at a rate that keeps pace (more or less) with the rate of growth of the fish. In fact, the determination of the ages of fishes by the markings on their scales, a familiar procedure in fisheries biology nowadays, is based on belief in the validity of this rule. But Hertwig's (1874, p. 358) observation that new dermal denticles are formed between pre-existing ones in some sharks,[1] not only during embryonic development but during later life as well, shows that the situation is not so simple for elasmobranchs.

Counts of about twice as many denticles within a given percentage of the total length of a specimen, below the first dorsal fin, of *C. coelolepis* 565 mm., 690 mm., and 1035 mm. long as on an embryo of 277 mm. (for details, see p. 49) show that the final number is developed, in this particular species, by the time a given specimen is about half grown — how much earlier is not known. It also seems evident, from the shapes and relative sizes of the denticles, and from their irregular arrangement, that several generations of them are represented on small examples as illustrated by our specimens of 565 and 690 mm. (Fig. 2, *B*, *C*). But the uniformity in size and shape of the denticles on adults, and the regularity with which they are arranged, suggest that the ovoid ones that first develop on specimens a little more than half grown represent the final generation, which persists throughout the later life of the individual concerned. We can go no farther than this from information available up until this time.

We think it probable, too, that a similar succession in the shapes of the denticles takes place between young specimens and adults, in the case of *Centroscymnus owstoni* Garman 1906, from Japan, a near relative of the North Atlantic *C. coelolepis*. When adult, its denticles resemble those of adult *coelolepis* very closely in shape. But they are tridentate over the trunk as a whole on two

[1] It is not clear, from the context, whether Hertwig made these particular observations on *Mustelus*, on *Acanthias*, on *Dalatias* or on *Heptranchias*.

Japanese squalids, 260 mm. and 287 mm. long, in the Museum of Comparative Zoology, which agree very closely in all other respects (including very minute denticles, very oblique lower teeth, and no median tooth in the lower jaw) with two adult males of *owstoni*, 785 mm. and 805 mm. long, in the Museum. Incidentally, the two small specimens just mentioned came from Japan labelled *Scymnodon squamulosus*. But they differ sharply from *squamulosus* as pictured by its describer (Günther, 1878, pl. 2, fig. B) both in their very oblique lower teeth, and in pectorals reaching back as far as the level of the origin of the first dorsal fin, for the lower teeth of *squamulosus* are shown as nearly erect, and the tips of its pectorals as falling short of the level of the origin of the first dorsal by a distance about as great as the length of the snout in front of the mouth.

On the other hand, the successional history of the denticles of *Centroscymnus coelolepis* strengthens the specific validity of *C. cryptacanthus* Regan 1906, from Madeira, the denticles on the type specimen of which (about 700 mm. long) were tridentate with 3 parallel keels on the trunk anterior to the first dorsal, but "the others smooth, with rounded edges and with a rounded depression on the free surface of each" (Regan, 1906, p. 437).

Present realization that it is not safe to define species of sharks by the shape of their denticles — unless the ages of the specimens in question be taken into account — forces us, next, to conclude that the juvenile squalids, 330-462 mm. long on which Bigelow, Schroeder and Springer (1953, p. 233) based the new species *Scymnodon melas* actually represent nothing more than an early stage in the growth of *Centroscymnus coelolepis*. Thus their denticles correspond very closely to the smallest and most tridentate of those of our 565 mm. *coelolepis* (p. 49, Fig. 2*B*), though they contrast so strongly with the rounded denticles of the adult that we would never have guessed that they belonged to the same genus, much less to the same species, had it not been proven that the denticles of the young of *coelolepis* are similarly tridentate, to be replaced by ovoid ones later. The somewhat wider spacing of the denticles on the supposed *melas* than on partly grown *coelolepis* points merely to an earlier stage in the growth of the individuals. Neither can we find any better excuse for retaining the species, whether in proportional dimensions, in the fins, or

in the shapes and number of teeth. And while we had thought its black color distinctive, as contrasted with the chocolate hue of the adult *coelolepis*, embryos of the latter, of proven parentage, are a very deep blue, while half-grown males are black, with only a faint tinge of chocolate to forecast the color of the adult.

The previous records for this species for the western Atlantic have been scattered along the slope, from the Grand Banks of Newfoundland to the offing of Nantucket. It is therefore interesting — as it was unexpected — that the three caught by "Cap'n Bill II" were all taken between the offings of New York and Delaware Bay, as follows:

Length in mm.	Sex	Lat.	Long.	Depth in fathoms
1035	♀	38°41′N	73°01′W	570-610
690	♂	39°09′N	72°21′W	485-520
555	♂	38°43′N	72°56′W	630-675

Our failure to take *coelolepis* off Georges Bank, or off Nova Scotia, where it was reported so often by the halibut fishermen years ago (Bigelow and Schroeder, 1948a, p. 498), and where about 90 successful hauls were made in 1949, 1952 and 1953 at depths greater than 200 fathoms, including about 40 hauls deeper than 400 fathoms, is something we cannot explain.

Earlier captures of *coelolepis* in American waters were from depths of 150-250 fathoms — all of them made with hook and line. But we have already noted the likelihood that it would be found much farther down the slope in the western side of the ocean, as it is in the eastern, if fished for there with suitable gear. And the "Cap'n Bill II" trawlings bear out this expectation, by extending its known range in American waters down to 630 fathoms at least.

BATOIDS
Family RAJIDAE
Skates

Raja bathyphila Holt and Byrne 1908

The capture by "Cap'n Bill II" of a female *R. bathyphila*, 360 mm. long, on the seaward slope of Georges Bank (Lat. 40°04′N, Long. 68°34′W), at 370-450 fathoms in 1952, and of a

juvenile male of 370 mm. at a neighboring station (Lat. 40°10′N, Long. 68°16′W) at 490 fathoms, added to earlier locality records for it at one station off Chesapeake Bay, at 3 stations off southern New England, and at one station off Browns Bank, in depths of 885 to 1188 fathoms,[1] show that this deep water skate is generally distributed along the mid zone of the continental slope, between the offings of Chesapeake Bay and of southern Nova Scotia. Knowledge as to its status farther to the northeastward along the American slope is to be desired to tell us how wide the gap may be between the geographic ranges occupied by it in the western side of the Atlantic, and in the eastern, where it is known only from the Irish slope (type specimen), so far as we are aware.

The depths of capture recorded for it so far (370-1188 fathoms on the American slope, 673 fathoms on the Irish) suggest that its center of population lies deeper than 400-500 fathoms, with the upper limit little shoaler, if at all, than 350 fathoms.

The most distinctive character of *bathyphila* is that its entire lower surface is darker than the upper surface. Indeed, it is unique in this respect, among the skates that are known from the North Atlantic outside of the Gulf of Mexico. Within the Gulf it is paralleled in this respect by the newly described *R. fuliginea* Bigelow and Schroeder 1954. But the latter differs from *bathyphila* so sharply in a more convex anterior outline as well as in the prickliness of the lower surface of its tail and of the upper sides of its pelvic fins that there is little likelihood that the one species could be taken for the other. For a comparison of *bathyphila* with the several skates of the Pacific and Indian Oceans that are similarly dark colored below, see Bigelow and Schroeder 1953, p. 161.

A character, almost equally diagnostic for *bathyphila* among skates of its geographic province, but one that has not been stressed previously, is the narrowness of its mouth. In the four specimens that we have measured[2] the breadth of the mouth ranges from 4.9 to 5.9 per cent as great as the total length. The only other skates known from the northwestern Atlantic, outside of the Gulf of Mexico, that approach it closely in this respect are *Raja garmani* Whitley 1939 (about 5.7-5.9 per cent); *R. fyllae*

[1] For details, see Bigelow and Schroeder, 1953, p. 159.

[2] The two "Cap'n Bill II" specimens, and two others, the proportional dimensions of which are given in Bigelow and Schroeder 1953, p. 161.

Lütken 1887 (5.8 per cent in eastern Atlantic specimen, 6.1-7.0 per cent in four of the "Cap'n Bill II" specimens, 397-497 mm. long); and *Breviraja plutonia* (Garman) 1881 (5.1, 5.6 per cent, in two specimens taken off Jacksonville, Florida). And there is no likelihood of confusing *bathyphila* with any of these, quite apart from its coloration. Thus the anterior contour of the disc of *bathyphila,* half-grown and larger, differs widely from that of *fyllae,* and the arrangement of thorns and prickles is noticeably different in the two species, as we have pointed out elsewhere (1953, p. 159). The plain coloration of the upper surface of *bathyphila* contrasts as strikingly with the pattern of dark rosettes on *garmani* as does the dark lower surface of *bathyphila* with the pale lower surface of *garmani.* And no one, we fancy, would be likely to mistake a *bathyphila,* wedge shaped in front, with tail only moderately long, and a hard snout, for a *plutonia,* with its much more convex anterior outline, much longer tail and soft snout.

The male *bathyphila* taken in 1953 has six large thorns along the mid line of the back from the scapular region to the level of the axils of the pectorals, with the single median row reaching back as far as the axils of the pelvics; the female has seven large medians between scapular region and level of axils of pelvics, rearward from which there are 2-3 less regular rows. Thus these specimens, 370 and 360 mm. long, respectively, represent a stage in development between the 463 mm. female pictured by us in Part 2 of Fishes of the Western North Atlantic and the somewhat smaller (323 mm.) male (1953, Figs. 30, 31A). They agree so closely with our earlier account of this species in all other respects that no further discussion of them seems needful from the taxonomic standpoint.

Raja fyllae Lütken 1887

This skate was included in our general survey of the rajids of the western North Atlantic (Bigelow and Schroeder, 1953, p. 194) because of its presence in west Greenland waters, where it has been known for many years, as it has in boreal and subarctic latitudes in the eastern side of the Atlantic. The cruises of "Cap'n Bill II" have now extended the known range of *fyllae* to the Nova Scotian slope, and even to the southwestern slope of

Georges Bank, in depths of 290-600 fathoms. It must, indeed, be very generally distributed (though in small numbers) along this depth zone between the offing of Halifax and the seaward slope of Browns Bank (longitudes 63°47′W to 65°06′W) for it was taken in 8 of the 19 successful hauls that were made there in 1952 (16 specimens) as well as in 8 of the 16 successful hauls

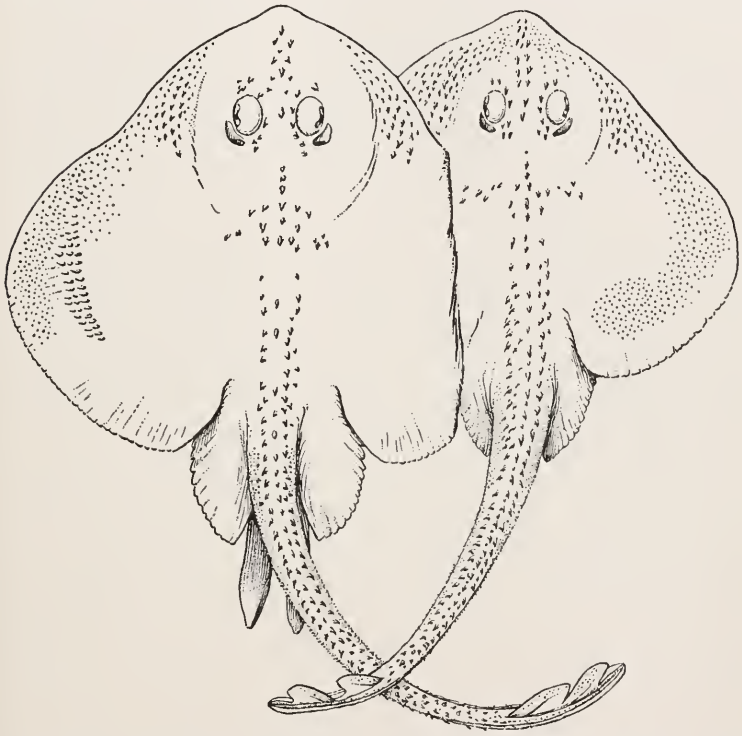

Fig. 3. *Raja fyllae*. *Left*, male, 505 mm. long, off La Have Bank, M.C.Z. No. 37905; and *right*, female, 430 mm. long, same general locality, M.C.Z. No. 37898.

made there in 1953 (13 specimens). And we may expect it to prove equally widespread around the Newfoundland Banks when the 300-600 fathom depth zone has been explored there more fully. But it seems to be much less numerous farther to the westward — unless at a considerably greater depth — for only

three hauls (3 specimens) yielded it on the Georges Bank slope (longitudes 67°02′W to 68°54′W), out of the 24 successful hauls that were made in 1952 and 1953, combined, at depths greater than 300 fathoms, between longitudes 66°W and 70°W. And it was not taken at all in the many hauls made farther to the westward and southward.

The Nova Scotian-Georges slope specimens (Fig. 3) agree so closely with the specimen from southwest of Ireland, figured by us (Bigelow and Schroeder, 1953, Fig. 39), both in shape of disc, in proportional dimensions including length of tail, and in dermal armature, that no cleavage is apparent between the populations inhabiting North American and north European waters. But the additional material allows us to expand our earlier description of the species in the following particulars.

A — Length of tail. In 7 of the larger specimens, 407-505 mm. long, including 2 mature males, the tail, measured from the center of the cloaca, occupies 58-61 per cent of the total length, and the ratio between length of tail and length of body is between 1.35 and 1.56. In 5 juveniles of both sexes, 198-272 mm., this ratio is 1.69-1.80. In *R. erinacea* and in *R. ocellata* (only skates with which *fyllae* might be confused in American waters) the ratio, length of tail to length of body, is about 1.00-1.35.

B — Shape of disc. The anterior contour of an adult male 505 mm. long, in the "Cap'n Bill II" series (Fig. 3) parallels closely that of a somewhat larger male (555 mm. long) from West Greenland that was pictured first by Lütken (1898, Pl. 2), and subsequently by Clark (1926, Pl. 22, fig. a) in being deeply concave on each side, abreast of the spiracles, a point worth mentioning since these are the largest males that have yet been seen, so far as we are aware. Females from off Nova Scotia, 397 and 430 mm. long, agree very closely in the shape of their discs with a female of 452 mm. taken southwest of Ireland that we have pictured elsewhere (Bigelow and Schroeder, 1953, p. 195, Fig. 39).

Students of skates have learned, long since, to expect considerable variation in dermal armature from specimen to specimen in nearly every species, both for the larger thorns and for the smaller prickles as well, though each species shows a basic arrangement that is characteristic of it. Our predecessors have

observed, already, that *fyllae* is no exception to this rule; and the Nova Scotian specimens afford an additional illustration. Thus the areas bare of prickles that tend to develop on the upper surface of its disc, as this skate grows, vary considerably in their extent among the females, independently of the sizes of the latter. In one, 430 mm. long, there is a bare area behind each spiracle, reaching rearward to the shoulder region, and there are no prickles on the upper surface of the pelvics. But the regions rearward from the spiracles are prickly on another female of 397 mm., and also the upper surface of the posterior lobe of each pelvic fin, much as they are on a female of about this same size taken off Ireland (Bigelow and Schroeder, 1953, Fig. 39), and in all of the smaller specimens of both sexes taken off Nova Scotia.

The males, as they mature, tend to lose any prickles they may have had earlier on the pelvics, and also to lose part of the larger thorns from the mid-dorsal belt of the disc between the levels of the pectoral girdle and of the axils of the pectorals.

It was known, previously, that the upper surface of the tail, which is set with prickles (besides the thorns) on small specimens, loses most of these prickles with growth. It now seems that this alteration is a more regular one than previous observations had suggested, for while the tail is uniformly and densely prickly above on the Nova Scotian juveniles, to 270 mm. long, it is wholly bare of prickles along a definite median band throughout its length back to the first dorsal fin on the larger Nova Scotian specimens of 397-505 mm. The shape, too, of the tail alters in *fyllae* with growth, from arched above in the young to flat above in adults, along the median band that has become bare of prickles.

A feature which seems to have escaped scientific attention is that the mucous pores on the nuchal region of *fyllae* are arranged in a pattern that is conspicuous on small specimens as well as on large. The only other skate of the western North Atlantic in which the pores in this region are noticeable is *R. laevis,* but they are black pigmented in the latter, whereas they are pale in *fyllae.*

Thirty to thirty-eight series of teeth have been recorded for *fyllae.* In the larger of the Nova Scotian specimens, 397-505 mm. long, the number of series varies more widely in the upper jaw (30-38) than in the lower jaw (30-32). It is not known whether

this same disparity obtains for the European population of this species.

The northeastern Atlantic and west Greenland representatives of *fyllae* so far seen have been ashy gray to chocolate brown above, the adults uniform, the young marked more or less distinctly with darker spots. One of the larger of the Nova Scotian females 430 mm. long, and 2 others half to three-quarters grown, are similarly of a uniform ashy gray tint above. But 5 other females are conspicuously marked, above, with an oblong whitish blotch, longer than wide, between the eyes, and with a similar but vaguely outlined pale blotch on the inner posterior part of each pectoral fin, a pattern of which we find no previous report for *fyllae*. One large male and 1 half grown lack these blotches but 1 large and 2 half to three-quarters grown males are so marked for *R. fyllae*. The lower surface is uniformly grayish white on the largest Nova Scotian male (505 mm.) both on tail and on disc. But the lower surface of other large specimens is more or less smoky around the outer posterior edges of the pectorals, in the region of the cloaca, and on the anterior parts of the pelvics; their tails are variously dark-blotched or mottled below; the region of the gill openings is smoky on one of them; and there is a smoky prepelvic blotch on three of them. Thus the dark markings on the lower surface vary as widely from specimen to specimen in extent and in arrangement among the Nova Scotian population as among the Greenland and eastern Atlantic populations.

The fact that the claspers are small, still, on one "Cap'n Bill II" male of 442 mm., but seem ready to function on another of 505 mm., on which the alar thorns have also developed in 2-3 rows, suggests that males of the Nova Scotian population mature, sexually, at a length of perhaps 475-500 mm.

The only other western North Atlantic skates that *fyllae* resembles closely in shape of disc, and in the general arrangement of its dermal armature, are *R. erinacea* Mitchill 1825, and *R. ocellata* Mitchill 1815. We have pointed out already (1953, p. 196) that it differs from both of these in a longer tail. But the measurements of the *fyllae* that we now have at hand show that the distance from the axils of the pelvics to the first dorsal fin as employed in our key (1953, p. 150) is not as reliable a criterion

as it seemed. Thus, while this distance is greater than from axils of pelvics to fronts of orbits in most of our *fyllae*, it is only about as great as to the mid levels of the orbits in a few, and is somewhat shorter than to the rear edge of the orbits in one adult male,[1] as it is in *erinacea* and *ocellata* also. And while the total length of the tail (measured from center of cloaca) is the greater relative to the length of the body in *fyllae*, there is virtually no discontinuity in this respect, as appears from the following table.

Ratio, total length of tail (from center of cloaca) to length of body

	max.	min.	average	number of specimens	total lengths mm.
fyllae	1.80	1.35	1.57	12	198—505
erinacea	1.35	1.06	1.22	9	209—505
ocellata	1.10	0.97	1.05	4	414—809

The distance, however, from the origin of the first dorsal fin to the center of cloaca is longer than from the cloaca to the tip of the snout in all the specimens of *fyllae* that we have measured, but shorter than from cloaca to snout both in *erinacea* and in *ocellata*, as follows:

Ratio, distance from first dorsal to cloaca relative to distance, cloaca to tip of snout

	max.	min.	average	number of specimens	total lengths mm.
fyllae	1.36	1.03	1.19	10	202—505
erinacea	0.97	0.81	0.88	5	209—505
ocellata	0.79	0.71	0.74	5	423—641

The interorbital space is narrower on *fyllae*, averaging 6.73 per cent (6.12-7.30) of the width of disc on 13 specimens examined, than it is on *erinacea* with an average of 8.01 per cent (7.32-8.50) on 11 specimens, or *ocellata* with an average of 9.12 per cent (8.82-9.32) on 4 specimens.

For specimens that cannot be identified, positively, by length of tail alone, the teeth should usually prove diagnostic, for there are only 30 to 38 series in the upper jaw in *fyllae* contrasted with

[1] Abnormal?

38 to 64 in *erinacea,* and 72 to 110 in *ocellata.* And the arrangement of the thorns on the tail usually is distinctive for large specimens, and in most cases for half grown, for *ocellata* and *erinacea* of these sizes usually have a narrow naked band along the mid line which has not been the case in any *fyllae* we have seen. But we must admit that specimens might come to hand for which depth of capture would be the only reliable criterion for identification that we have been able to discover.

In any case there is little danger of confusing *fyllae* either with *erinacea* or with *ocellata* in the field, for it has never been taken in North American waters shoaler than 290 fathoms, and neither of the others deeper than 85-87 fathoms (two *erinacea* trawled by "Cap'n Bill II" off the southern edge of Georges Bank in July 1953).

Raja jenseni Bigelow and Schroeder 1950

The captures of a female *jenseni,* 625 mm. long and in good condition, by "Cap'n Bill II" on the slope of Browns Bank, Lat. 42°19′N, Long. 64°59′W, in a trawl haul at 390-440 fathoms, and of a second female, of 695 mm., off Delaware Bay (Lat. 38°47′N, Long. 72°54′W) at 585-595 fathoms, call for mention, for the only specimens of this deep water skate that had been reported previously were a male, of 223 mm. from the slope of Georges Bank, 1255 fathoms; a female (the type) of 541 mm. off southern New England, 1043 fathoms; and a female of 850 mm. (now fragmentary) from off Halifax, Nova Scotia, brought in by a fisherman from 200 fathoms;[1] all are now in the U. S. National Museum, and all were taken many years ago.

The "Cap'n Bill II" specimens agree so closely with the type specimen (Bigelow and Schroeder, 1950, Pl. 1; 1953, Fig. 45) that their specific identity is evident at a glance. There are 29 large thorns in the mid dorsal row on the 625 mm. female, 8 of them anterior to the level of the axils of the pectorals. On the 695 mm. specimen, the total number in the median row is 26, 6 of which are anterior to the level of the axils of the pectorals, so spaced as to suggest that 3 or 4 others had been lost. These counts contrast with a total of 24 or 25 on the type (7 anterior to

[1] For the nomenclatural history of *jenseni,* description, and illustrations, see Bigelow and Schroeder, 1950, p. 385, Pl. 1; 1953, p. 213, Figs. 45, 46.

the axils of the pectorals) and with a total of 31 on the smaller male (8 anterior to the axils of the pectorals). Evidently there is a small variation in number from specimen to specimen, independent of the sizes of the latter. Enough specimens have been seen to show that it is characteristic of *jenseni* for the mid-dorsal thorns to be widely spaced anterior to the pelvic girdle, but increasingly closely spaced thence rearward onto the tail. On the 625 mm. female the thorns on the disc are about 20 mm. apart; those abreast of the axils of the pelvics about 10 mm. apart. The next 8 thorns along the tail are in contact at their bases, but the thorns thence rearward are separated, one from the next, by short interspaces. Also, the thorns are successively smaller, rearward along the posterior third of the tail. As on the type, there is no thorn in the interspace between the two dorsal fins on either of the "Cap'n Bill II" specimens, but only a few prickles.

The presence, on each side, of 3 or 4 thorns on the scapular region on the small male of 223 mm., and of 3 on the type, 541 mm. long, but of 2, only, on both of the "Cap'n Bill II" specimens of 625 mm. and 695 mm. indicates that one or two of the thorns in this group are lost with growth. There may be either two postocular thorns or three on different specimens,[1] but every specimen that has been seen has had one preocular thorn, only, on each side. The tip of the snout and the rostral ridge are about as rough on the "Cap'n Bill II" specimens as on the type, and the small prickles are about as densely distributed and cover about the same areas. A point worth emphasis is that while the sides of the tail of *jenseni* are densely prickly there are no prickles on the lower surface of its tail below the level of the lateral folds. The lower surface of the disc is naked everywhere.

Fifty-eight and sixty-six series of upper teeth have been reported previously, for the two specimens for which they have been counted. The "Cap'n Bill II" female 625 mm. long has 60, but the 695 mm. specimen has only 51. Evidently the number is widely variable on this species, irrespective of size, much as in *R. erinacea,* and in *R. ocellata.* The teeth resemble those of the type specimen closely (Bigelow and Schroeder, 1953, Fig. 46D) both in shape and in arrangement.

[1] Three on the 850 mm. female; two on each of the other specimens that have been examined.

We have forecast already that the dark markings on the lower surface of the disc, in *jenseni*, would prove widely variable (Bigelow and Shroeder, 1953, p. 216), and the "Cap'n Bill II" specimens corroborate this expectation. The ground-tint in both cases is yellowish white. On the 625 mm. specimen this is clouded with ashy gray around the posterior marginal zone of the pectorals and on the outer posterior parts of the pelvics; in the region of the cloaca and forward on either side of the abdomen; also over an irregular area on each side close behind the mouth. On the 695 mm. female the lower surfaces of the pelvics, the abdominal region in general, the lower surfaces of the pectorals, an irregular area on either side inward and forward from the gill region, and another smaller, inward from the nostril, are dark sooty gray. This pattern simulates, rather closely, the dark markings on some specimens of *R. hyperborea* (Bigelow and Schroeder, 1953, p. 209, Fig. 44), from which *jenseni* differs quite sharply by having a more simple dermal armature and fewer teeth (Bigelow and Schroeder, 1953, p. 213). The lower surface of the tail has been plain dark ashy gray on all the specimens of *jenseni* that have been seen thus far.

The localities whence *jenseni* has been reported (see above) are scattered sufficiently to show that it is generally distributed along the upper part of the slope between the offings of middle Nova Scotia and of Delaware Bay. But we have yet to learn how much farther its geographic range may extend in either direction. And the paucity of captures, with the great depths at which the "Albatross" specimens were taken, suggests that while a sparse population exists as shoal as 200-600 fathoms, the center of abundance for this species lies deeper down the slope than has been sampled yet by adequate methods of fishing.

Raja laevis Mitchill 1817
Barn Door Skate

This skate has been recorded as deep as 235 fathoms, but it occurs most regularly, and in greatest numbers on the continental shelf in depths shoaler than 70-80 fathoms. Hence captures of it by "Cap'n Bill II" at 265-305 fathoms off Nova Scotia (2 specimens in 2 hauls, Lat. 42°23′—42°28′N; Long. 64°31′—

64°52′W), and at 300-410 fathoms off Nantueket (1 specimen in 1 haul, Lat. 39°54′N, Long. 69°56′W) are of interest, as extending the known depth-range of the species downward, somewhat.

Other records of it, from the trawlings of 1952 and 1953 were from 220-255 fathoms on the seaward slope of Georges Bank (1 specimen, Lat. 40°11′N, Long. 68°20′W), and from 175-225 fathoms off southern New England (1 specimen, Lat. 40°04′N, Long. 72°12′W, 190-225 fathoms, and 2 specimens in 1 haul, Lat. 39°56′N, Long. 71°22′W, 175-200 fathoms).

Raja mollis Bigelow and Schroeder 1950

The type—and only known—specimen of this species, trawled on the slope off southern Nova Scotia, Lat. 41°53′N, Long. 65°35′W, at a depth of 858 fathoms by the "Albatross" in 1883, had rested, unnoticed, in the U. S. National Museum until 1950. We can now add three more records for *mollis* from that same general region, namely, a juvenile male, in the neighborhood of 195 mm. long (tip of tail lost) taken by the "Caryn" in June 1949, at Lat. 41°25′N, Long. 65°54′W, in a trawl fishing between 415 and 490 fathoms; a second male, of 267 mm. taken by "Cap'n Bill II," July 26, 1952, at Lat. 42°40′N, Long. 63°51′W, from 465-480 fathoms; and a third, 298 mm. long, July 12, 1953, from Lat. 42°40′N, Long. 63°52′W, at 415-420 fathoms.

The fact that "Caryn" and "Cap'n Bill II" took only three specimens of *mollis* in the 39 hauls they made at depths deeper than 300 fathoms in the Nova Scotian sector during the three summers combined, coupled with the depth (850 fathoms) at which the type specimen was trawled, makes it likely that the center of population for this species is along the lower part of the continental slope. But it is anyone's guess how far its geographic range may extend, either to the northeastward, or to the southwestward.

Mollis falls in the moderately short-tailed subdivision of the genus, the distance from the level of the axils of its pelvics to the first dorsal fin being much shorter than from the axils of the pelvics to the tip of the snout, and the total length of its tail from the cloaca being only about 1.1 times as long as the body from center of cloaca to tip of snout. Its most noticeable external characteristics are that it has no large thorns anywhere, posterior

to the scapular region, but that the upper surface of its disc and tail are densely prickly, except close along the outer posterior edges of the pectorals, and that the entire breadth of the lower surface of its tail is also densely prickly, except for the extreme tip.[1] The only slight differences worthy of mention between the larger of the two "Cap'n Bill II" specimens and the type is that the former has two minute thorns close in front of each eye (only one in front of each eye on the type); and that while there is a very small postocular thorn (as on the type) on one side of its head, none is to be seen on the other side among the close-set prickles that roughen the skin there. There are 54 series of teeth in the upper jaw of the "Caryn" specimen about 195 mm. long, 60 in both the "Cap'n Bill II" specimens of 267 and 298 mm., and 60 on the type specimen.

On the type specimen, the rostral projection from the cranium, reaching nearly to the tip of the snout (easily felt) is soft throughout its length. It is soft on the "Cap'n Bill II" specimens also and this state is so unusual, among the members of the genera *Raja* and *Breviraja*, that we considered it as perhaps the outstanding feature of the species *mollis*, in our earlier discussion (1953, p. 237). But the rostral cartilage of the very small specimen (195 mm. long) collected by "Caryn" in 1949 is rather stiff to the touch, raising the question as to whether its degree of firmness is a matter of the stage in growth, or whether it perhaps is affected by preservation.

Raja radiata Donovan 1807
Thorny Skate

Previous knowledge of the range of the thorny skate, and the numbers in which it has been taken on the Newfoundland Banks, in the inner parts of the Gulf of Maine, and on Georges Bank (Bigelow and Schroeder, 1953, p. 262) had led us to expect a plentiful representation of this species among the catches that were made off Nova Scotia, and along the seaward edge and slope of Georges Bank by the "Cap'n Bill II" in 1952 and 1953. But the results proved otherwise for it was taken in 10 hauls, only, in these two sectors combined, out of a total of 51 hauls that fished

[1] For detailed comparison with other species of *Raja*, see our earlier account (1953, p. 237).

successfully there between 120 fathoms and 400 fathoms and none was caught in 34 deeper hauls. The total number of specimens, too, was only 12, the maximum catch in one haul only 2. This, contrasted with the large catches that have been made on the Newfoundland Banks, on Georges, and in the western side of the Gulf of Maine (Bigelow and Schroeder, 1953, p. 262) is evidence that while it has been taken as deep as 430-490 fathoms off New York by "Cap'n Bill II" (Lat. 39°26′N, Long. 72°12′W, July 1953) and at 459 fathoms near Spitzbergen, its center of abundance lies shoaler than the zone along which the great majority of the "Cap'n Bill II" hauls were made. But the sizes of the specimens taken at different depths make it likely that the thorny skate reproduces itself, indifferently, down to the greatest depth to which it occurs, for those taken shoaler than 300 fathoms ranged from 196 mm. to about 860 mm. in length, those taken deeper, from 145 mm. to about 865 mm. And while one from 240-270 fathoms contained an egg about ready for deposition, another from 400-460 fathoms contained a mass of immature eggs.

This skate was taken at 8 stations out of 44 along the 120-400 fathom depth zone off southern New England in the two years combined; but, again, the largest catch was only 2 specimens, the total catch 11 and only 1 was caught in 26 stations deeper than 400 fathoms. Five specimens, also, were taken in 3 hauls fishing between 253 and 490 fathoms off Long Island, New York (longitudes 72°12′-72°19′) in June-July 1953 (it had been reported nearer land there, previously). But it seems that the so-called "Hudson Trough" off New York about marks the boundary to its regular occurrence in that direction at any depth, for "Cap'n Bill II" did not take it in any of the hauls that she made southward thence to the offing of Virginia in the summer of 1953, though we have seen a specimen from 74 fathoms off Charleston, South Carolina (Bigelow and Schroeder, 1953, p. 263).

Raja senta Garman 1885

This skate, ranging from the Newfoundland Banks and the inner part of the Gulf of St. Lawrence to the offing of South Carolina, was already known to occur widespread, though in small numbers, from the offing of western Nova Scotia to the offing of

New Jersey; chiefly between 50 fathoms and 250 fathoms, but recorded as deep as 478 fathoms off South Carolina. Therefore, it was no surprise to take 1-2 specimens in each of 6 hauls at 125-340 fathoms along the slope of Georges Bank (Long. 66°51′W and 69°43′W), 1 or 2 in each of 7 hauls at 150-225 fathoms off southern New England (Long. 70°-72°01′W), 1 off Maryland (Lat. 38°38′N, Long. 73°10′W), at 190-200 fathoms, and 1 off Virginia (Lat. 37°38′N, Long. 74°14′W) in 1952 and 1953. The series ranges from 120 mm. in length to about 577 mm.; the largest is a male with well developed claspers.

Raja spinicauda Jensen 1914

Definite locality records for this cold-water skate had been limited, previously, to Barents Sea, to the waters east of Iceland, to southwestern Greenland and the Greenland side of Davis Strait, to the continental slope off eastern Newfoundland, and to Hermitage Bay on the southern Newfoundland coast. But the fact that an egg case, apparently of this species to judge from its external sculpture and from the embryo contained within it, had been brought in from Banquereau Bank, and that a similar case (empty) had been trawled on the southwestern slope of Georges Bank,[1] had made it likely that the range of *spinicauda* extended southward and westward along the upper part of the continental slope as far as the general offing of Cape Cod. And this likelihood has now been corroborated by the capture of a juvenile male 392 mm. long by "Cap'n Bill II" on the slope of Georges Bank (Lat. 42°17′N, Long. 65°06′W) at 320-360 fathoms, besides two egg cases (one with identifiable embryo) off southern Nova Scotia (Lat. 42°44′N, Long. 63°17′W, 410-420 fathoms) in 1952, and of a third egg case, with well advanced embryo, on the slope of Georges (Lat. 40°43′N, Long. 66°42′W, 405-430 fathoms) in 1953.

Spinicauda had been recorded previously from 77-88 fathoms (140-160 meters) off Iceland, 120-404 fathoms off west Greenland, and 120-140 fathoms in Newfoundland waters. The depths recorded for the partly grown male taken by "Cap'n Bill II" in 1952 (320-360 fathoms), as well as for the egg cases taken

[1] See Jensen (1948, pp. 50-52, and 53, Fig. 3) for records for Barents Sea, Iceland and Greenland; Bigelow and Schroeder (1953, p. 272, 276) for those for American waters.

by "Caryn" in 1949 (260-350 fathoms) and by the "Cap'n Bill II" in 1952 and 1953 (405-430 fathoms) suggest that *spinicauda* occupies a somewhat deeper zone in the southernmost part of its range than in the northern part.

The bottom temperature was 3.3° in 1953, at the only locality where *spinicauda* was taken (egg case with embryo) that summer, and 3.9°-4.4° along the general depth zone where either free-living *spinicauda*, or its egg case, was taken in 1949 or in 1952, years when the temperature was not recorded. These values suggest that the upper limit to its thermal range may be slightly higher off Georges Bank and off Nova Scotia than off the east coast of Newfoundland, where the bottom water, at the depth where it was taken (91-127 fathoms) was between −1.5° and +0.65°, or in west Greenland and Icelandic waters where it has been found in temperatures of 1.7° to 3.8°.

Spinicauda is given so distinctive an aspect by its wedge shaped anterior contour with very long snout, and by a generally prickly upper surface, but with larger thorns confined to a single row of 21-26 (three examined by us had 22, 23 and 24 thorns, respectively) along the mid line of the tail with one between the first and second dorsal fins, that it could hardly be mistaken for any other skate known from the western North Atlantic. The only noticeable respect in which our juvenile male differs from the adult is in a somewhat longer tail, a growth feature that also is known for several other skates. More in detail, the distance from the center of the cloaca to the first dorsal fin, relative to the distance from center of cloaca to tip of snout, is about 1.2 times as great on the "Cap'n Bill II" juvenile male, as on the mature male, 1,236 mm. long, from Newfoundland, the proportional dimensions of which are given in Part 2 of "The Fishes of the Western North Atlantic" (Bigelow and Schroeder, 1953, p. 272). And this divergence between small specimens and large is about what might have been expected; the corresponding ratio, for example, in length of tail between young and adult (measured similarly) is about 1.2-1.3 for *R. erinacea;* about 1.2 for *R. fyllae;* about 1.1 for *R. laevis;* 1.1-1.3 for *R. radiata;* and 1.1-1.3 for *R. senta.*

In the adult *spinicauda* the rostral projection from the front of the cranium (reaching very nearly to the tip of the snout)

is slender and rodlike along the anterior ¾ of its length, and its cartilaginous nature is evident, if the skin above it be slit, and its sheath of fibrous tissue be spread apart. It is of the same shape in our juvenile male. But in this case the histologic nature of its anterior part remains to be learned, for it is only close to the cranium that it is visible on an X-ray photograph. And we have not felt free to dissect the single specimen, or to treat it with a stain selective for cartilage.

Ishiyama (1952, p. 2) has already pointed out that X-rays must be used with caution as tests for cartilaginous skeletal elements in rajids. We have found, for example, that while the outlines of the cranium, of the jaw cartilages, of the vertebral column, and of the basal cartilages of the paired fins show clearly in our X-rays of various skates and rays, those of the pectoral fins may, or may not. Thus, the pectoral radialia are sharply outlined on our X-rays of *Gymnura,* but the only visible evidence of them on X-rays we have studied of various species of *Raja, Breviraja, Cruriraja, Psammobatis* and *Sympterygia* is along the narrow axial strands of calcification. Consequently, X-ray photographs can be relied on as tests for the length of the rostral cartilage only if they show its anterior termination sharply.[1]

The egg cases trawled by "Cap'n Bill II" in 1952 and 1953 — identity established by the embryos contained in them — resemble those referred provisionally to this species by Jensen (1914, p. 33; 1948, pp. 55, 56) and by us (1953, p. 272) very closely. They are unique so far as known, among the egg cases of Atlantic skates, in the sculpture of their surfaces with a large number of low, longitudinal ridges, each close-set with a single series of several hundred stiff rod-like structures with complexly dissected tips (Fig. 4).

The three egg cases we have examined measure about 90 by 130 mm.; about 92 by 135 mm.; and about 86 by 136 mm., not counting the terminal horns. The embryo that one of them contained, 185 mm. long to its first dorsal fin, and 242 mm. to the tip of its tail, still bears the large yolk sac. But it is so nearly ready for birth that its identity as *spinicauda* is obvious. Embryonic characters — still persisting — apart from the yolk sac are that only the tips of the single line of caudal thorns (22 in

[1] See, for example, Bigelow and Schroeder, 1948, Figs. 1, 2; 1953, Fig. 62.

number) show through the skin ; that the length of the tail, from center of cloaca to first dorsal fin, relative to the distance from center of cloaca to snout, is about 1.2 times as great as in the

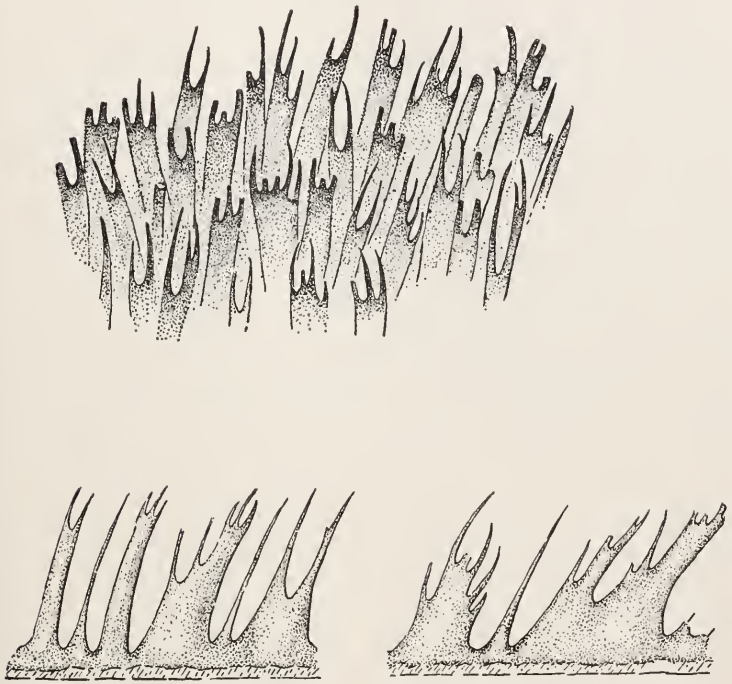

Fig. 4. *Raja spinicauda.* Portion of egg case trawled on the Nova Scotian slope in 410-420 fathoms, Lat. 42°44′N, Long. 63°17′W, M.C.Z. No. 37691, to show sculpture; above, about 7 x, below, about 11 x.

juvenile male of 390 mm. ; that the tip of the tail still carries the embryonic filament which with the caudal fin fold extends 35 mm. from the rear base of the second dorsal ; and that the thorn is not yet visible between the two dorsal fins.

CHIMAEROIDS

Family CHIMAERIDAE

Hydrolagus affinis (Brito-Capello) 1867
Deep Water Chimaera

This chimaera was described originally from deep water off Portugal. The first report of it, on our side of the Atlantic, was by Gill in 1878 (as *Chimaera plumbea* n. sp.), from one brought in from 350 fathoms off La Have Bank. So many of them were brought in during the next few years, by schooners long-lining for halibut, that Goode and Bean (1895, p. 31) characterized it eighteen years later as "very common in the deep water on the outer edge of the banks north of Georges Banks."[1] And while one specimen, only, is known to have been taken on the American slope during the past quarter century, we have risked the prediction that "it would be found on the offshore slopes in undiminished numbers if it were sought at the proper depth" (Bigelow and Schroeder, 1953, p. 544). This, then, was one of the fishes we expected the trawlings of "Caryn" and of "Cap'n Bill II" to yield. But they did not catch a single specimen. The failure to take this particular species can hardly be blamed on insufficient coverage of the zone explored, for 38 successful hauls reaching deeper than 200 fathoms were made along the slope of Georges Bank, 26 of which fished deeper than 300 fathoms, 19 deeper than 400 fathoms and 3 deeper than 500 fathoms; 49 hauls reaching deeper than 200 fathoms along the Nova Scotian slope, 39 of them deeper than 300 fathoms; 21 deeper than 400 fathoms and 7 hauls deeper than 500 fathoms, in the summers of 1949, 1952, and 1953 combined.

The fact that all reports of *affinis,* for the western side of the Atlantic, have been based on specimens caught with hook and line might suggest that our method of fishing was at fault. But the otter trawl is so efficient an apparatus that we think it more likely that *affinis* actually is far less numerous along the Georges Bank and Nova Scotian slopes today than it was, there, 50-70 years ago.

[1] For reports of it, in the Western Atlantic previous to 1953, see Bigelow and Schroeder, 1953, p. 544.

Family RHINOCHIMAERIDAE

Rhinochimaera and Harriotta

The most striking feature of these bizarre chimaeroids is their very long pointed snout, supported chiefly by the correspondingly long upper rostral cartilage. This cartilage follows the same course in *Harriotta* as is pictured for it in *Rhinochimaera* by Garman (1904, Pl. 1, fig. 2) and by Dean (1904, Pl. 1, fig. 4). We may add to our earlier account (1953, p. 549) that it is separated from the skin along the inner part of the snout by a mass of white, semigelatinous, pulpy tissue. The cartilage is in close contact with the overlying skin toward the tip of the snout for a short distance in *Rhinochimaera* of both sexes, also in females and young males of *Harriotta*, and for a longer distance in mature males of the latter, the tips of the snouts of which are hard. The cartilage as we have pointed out (1953, p. 549) is more flexible in the vertical plane around the crest of its curvature than elsewhere, so that it is easily bent down there mechanically, even on preserved specimens. But we have yet to learn whether the fish can direct the outer part of the snout upward or downward voluntarily.

Three genera of rhinochimaerids are known: *Neoharriotta* Bigelow and Schroeder 1950, type species *N. pinnata* (Schnakenbeck) 1929[1] (West Africa south of the equator), with separate anal fin; *Harriotta* Goode and Bean 1895 (North Atlantic, Japan, and off lower California) and *Rhinochimaera* Garman 1901 (North Atlantic and Japan), without separate anal. Characters that we have accepted previously (1953, p. 549) as alternative between *Harriotta* and *Rhinochimaera* are the nature of the dental plates (smooth in *Rhinochimaera* but with grinding ridges and knobs in *Harriotta*), and whether the upper margin of the caudal fin is smooth (*Harriotta*) or is armed with a longitudinal row of denticulate structures (*Rhinochimaera*). Examination of the representatives of each that were taken during the recent trawling trips of "Caryn" and of "Cap'n Bill II" shows that the first of these criteria can be relied upon, except for newly hatched specimens, the dental plates of which are smooth, or very nearly so in *Harriotta* as well as in *Rhinochimaera*. In fact we

[1]Given erroneously as 1931 in Bigelow and Schroeder 1953, p. 550.

have found no reliable feature to separate newly hatched specimens of the North Atlantic representatives of *Harriotta* and of *Rhinochimaera* generically, though it is easy to do so specifically. It proves, also, that the presence of denticulations along the upper side of the caudal fin is reliable as a distinctive criterion for adult males of *Rhinochimaera,* as contrasted with *Harriotta,* but not for young males, or for females, as is pointed out below (p. 80). And it must remain an open question, until growth series of *Rhinochimaera* can be studied, as to how early these denticulations develop. All we can say, in this regard, is that while the upper margin of the caudal is so thick and fleshy in adult *Rhinochimaera* of both sexes that the horny rays are entirely concealed, it is so thin on a female *R. atlantica* 457 mm. long that these rays are clearly visible. The development, also, of a double series of hard knobs along the terminal ⅕-¼ of the snout of maturing males in *Harriotta raleighana* and in its close relative *H. chaetirhamphus* (Tanaka) 1909, of Japan,[1] but not in *Rhinochimaera* seems more properly a generic character than a specific. Another character, not proposed previously as alternative, between *Harriotta* and *Rhinochimaera,* but which seems to be so, is the shape of the outer part of the long upper rostral cartilage which is subtriangular (base uppermost) in cross section in *Harriotta* but is nearly as thick along its lower side as along its upper side in *Rhinochimaera.*

Rhinochimaera atlantica Holt and Byrne 1909

This chimaeroid, previously known from the type specimen only, from the Irish Atlantic slope, and from a few empty egg cases presumably referable to it, was represented by 8 specimens in the "Cap'n Bill II" collections. These range from a newly hatched male, 151 mm. in total length, to large adults of both sexes 1060-1315 mm. long. According to Holt and Byrne (1910, p. 19, Pl. 3) *atlantica* differs from *pacifica* (Mitsukuri) 1895, of Japan, in a relatively shorter second dorsal fin, which they picture as shorter than the distance from the gill openings to the origins of the pelvic fins, but which they characterize as longer

[1] The illustration of the only other member of the genus, *H. curtis-jamesi* Townsend and Nichols 1925, from off lower California (Townsend and Nichols, 1925, Fig. 2) suggests that the specimen was a female; and in any case it was too small (6 inches) to show this character, even if actually a male.

than that distance in *pacifica*, as it is shown on Dean's (1904, Pl. 1, fig. 1) illustration. But the second dorsal of *pacifica* is shown as only about as long as from gill opening to pelvic origin by Mitsukuri (1895, Pl. 1), and as shorter than that distance by Garman (1904, Pl. 1, fig. 1). The ratios, tabulated below, between length of base of second dorsal and distance from gill opening to pelvics, for the "Cap'n Bill II" series of *atlantica,* and for two specimens of *pacifica* in the Museum of Comparative Zoology (one of these was the basis of Garman's illustration) are further evidence that the Atlantic population cannot be separated from the Japanese on this basis. And we may note, in passing, that the point of origin cannot be located with precision either for the second dorsal, or for the pelvics because of the shapes of these fins.

Species	Length, to rear base of 2nd dorsal mm.	Sex	Ratio, base 2nd dorsal to distance gill opening to pelvics
atlantica	727	♂	1.0 : 0.98
"	755	♂	1.0 : 1.09
"	770	♀	1.0 : 1.0
"	825	♀	1.0 : 1.08
"	856	♀	1.0 : 1.0
"	*880	♀	1.0 : 1.0
pacifica	575	♂	1.0 : 1.0
"	590	♂	1.0 : 1.0

According to Holt and Byrne (1910, p. 19, Fig. 3, and Footnote) a second difference between *atlantica* and *pacifica* is that the "posterior limbs" of the forked canal that runs rearward along the lower surface of the snout, end blind in *atlantica*, but join the median anterior loop of the angular canal[1] in *pacifica.* Examination, however, of the two specimens of *pacifica* in the Museum of Comparative Zoology shows that they actually end blind in that form, as they do in *atlantica*, though the blind termination may lie very close to the median loop of the angular canal, on one side of the head or the other, on some specimens, both of *pacifica* and of *atlantica,* perhaps on both sides in some cases. Garman's (1904, Pl. 2, fig. 2) illustration of the lower

[1] Nomenclature according to Garman (1888) and Bigelow and Schroeder (1953, p. 530, Fig. 119A).

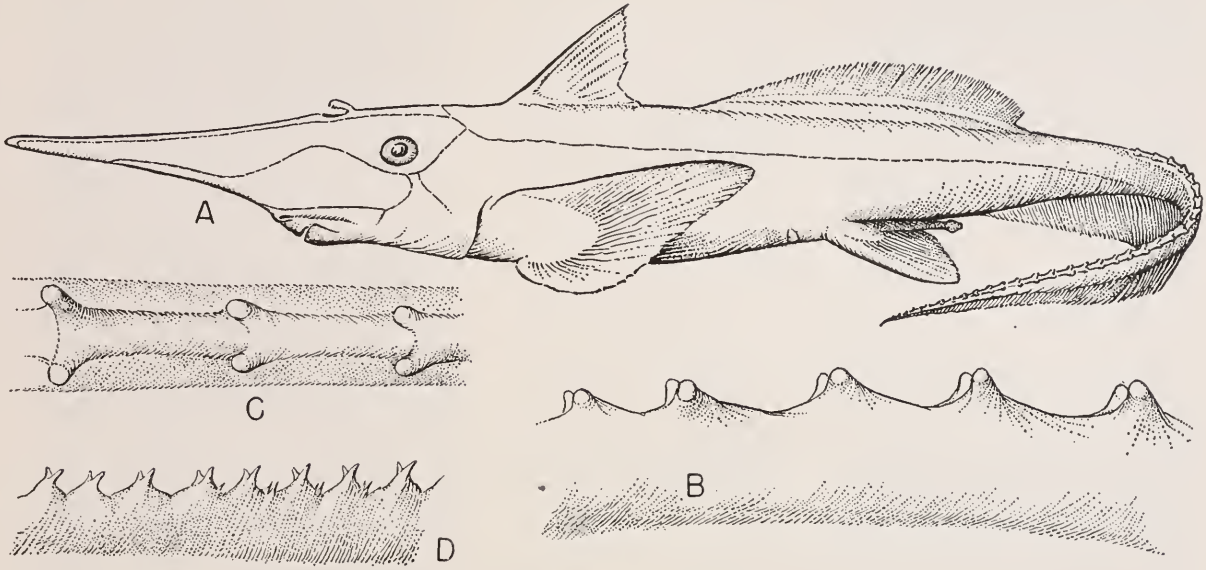

Fig. 5. *A, Rhinochimaera atlantica* Holt and Byrne, 1909, adult male, 1130 mm. long to upper termination of caudal fin. Nova Scotian slope. M.C.Z. No. 38244. *B* and *C,* Lateral and dorsal views of upper margin of anterior part of caudal fin of same, to show the tubercles, about 1.7 x. *D, Rhinochimaera pacifica,* adult male, 885 mm. long, Japan, M.C.Z. No. 1314, side view of upper margin of anterior part of caudal, about 1.7 x.

surface of the snout of *pacifica* is not clear in this respect.

Neither have we found anything to differentiate the Atlantic form (Fig. 5) from the Japanese, either in proportional dimensions, in the shapes, sizes or relative positions of the fins, in the nature of the dorsal spine (described for *atlantica* on p. 76), or in the shapes of the dental plates, which are as free from any trace of grinding prominences in the one as in the other. But our specimens do suggest that the caudal filament may average significantly longer on Japanese specimens than on Atlantic. Thus it is almost as long as the second dorsal fin in one of our *pacifica* and is pictured as about 70 per cent as long as that fin by Dean (1904, Pl. 1, fig. 4), whereas it is only about 10 per cent as long as the base of the second dorsal on one of our *atlantica* specimens on which it seems to be intact, while it is pictured as very short, indeed, by Holt and Byrne (1910, Pl. 3) for the type specimen. It seems, too, that the denticulations (single or paired) with which the upper margin of the caudal fin is armed, on large specimens, are not only more numerous on the Japanese form than on the Atlantic, but that they are regularly present on the females of the former, as well as on the males, but only on some of the females of the latter. Thus there are 47 and 52 series, respectively, on the two adult males of *pacifica* that we have examined, with "over fifty" reported for it by Dean (1904, p. 6), while his illustrations of an adult female (Dean, 1904, Pl. 1, figs. 1, 4) show them as rather prominent and as distributed continuously all along the caudal. But they number only 25 and 30, respectively, on our two adult Atlantic males; only one of our four large Atlantic females shows traces of them all along the caudal; the caudals of two of them are perfectly smooth; and they are much smaller on females where they are to be detected at all than they are on adult males. On the other hand, they are larger, relatively, on the large Atlantic males (Fig. 5) than on the Japanese.

In estimating the taxonomic significance of these differences, we face the puzzling fact that the caudal denticulations of one of the Japanese males resemble those of the Atlantic males in their low, rounded form, with the interspaces smooth edged between them. But they are sharp pointed (whether single or in pairs) on the other Japanese male of about the same size, with the interven-

ing spaces interrupted, in most cases, by 1-3 much smaller, pointed denticles, as pictured by Garman (1904, Pl. 4, fig. 2) many years ago for this same specimen, and by us more recently (1953, Fig. 122).

It must remain an open question, until half-grown males can be examined, whether this difference between two specimens, both of which seem to be mature, represents two extremes of individual variation, or whether one of these conditions (and if so, which of them) precedes the other, as a given male becomes active, sexually.

To sum up, the North Atlantic population of *Rhinochimaera* seems to differ certainly from the Japanese only in a secondary sexual character that is subject to considerable variation from specimen to specimen, and perhaps in the proportional length of a structure (caudal filament) so susceptible to damage that estimates of its length are largely a matter of guesswork for a large proportion of the specimens that have come to hand. Were we facing the question *de novo* we would hesitate to separate the Atlantic form from the Pacific, specifically, on such slender bases. However, since the name *atlantica* is in use already, we are content to let it stand for the time being. Reduction to the rank of subspecies may be its ultimate fate.

The general morphology of *Rhinochimaera pacifica,* internal as well as external, was made well known by Garman's (1904) and Dean's (1904) studies, accompanied by beautiful illustrations. The following details for *atlantica,* additional to Holt and Byrne's (1910) account, are based on the "Cap'n Bill II" specimens.

The rear edges of the dorsal fin-spine are perfectly smooth on all the large specimens, as noted by Holt and Byrne (1910, p. 18). But they are rough with minute serrations along the outer third of their length on a female 457 mm. long; evidently they are lost during later growth. Holt and Byrne's illustration (1910, Pl. 3) suggests, further, that the spine is attached to the fin right out to its tip (they do not comment on this), not free toward the tip as it is in *Harriotta* (p. 83). And this seems to be the normal state, being true of one of our large females, and of the largest male as well. But the union must be a feeble one, for the membrane is free from the fin along its outer ⅓-⅔ on all our

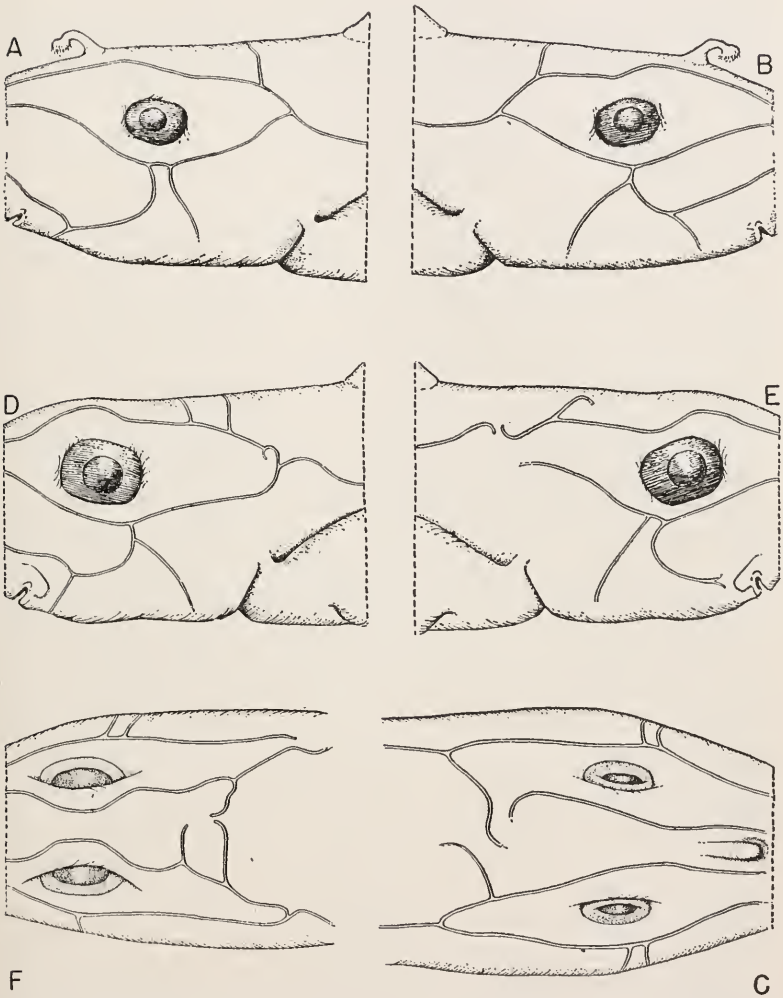

Fig. 6. Diagrams showing pattern of mucous canals on head. *A*, *Rhinochimaera atlantica*, same specimen as in Figure 5, left side. *B*, Same specimen, right side. *C*, Dorsal view of male, 1034, mm. long to upper termination of caudal fin, M.C.Z. No. 38243. *D*, *Harriotta raleighana*, female, 840 mm. long to upper termination of caudal fin, M.C.Z. No. 38247, left side. *E*, Same specimen, right side. *F*, Same specimen, dorsal view.

other specimens, including a female only 450 mm. long, without any clear sign that the separation had been a forcible one.

Our specimens corroborate Holt and Byrne's (1910, p. 21) suggestion that the pattern of mucous canals on the sides of the head is a variable character, as it is in *Harriotta* (p. 83). It seems usual for the jugular canal and the oral canal to branch off separately from the orbital canal below the eye, with the two separated by a longer or shorter interspace. But it is only on one side of the head that this is the case on one of the large females, and on one of the large males; on the other side of the head of each of these individuals the jugular canal and the oral canal branch from the orbital as a single trunk which bifurcates some little distance outward from its point of departure from the orbital (Fig. 6*A*, *B*). It proves, too, that the canal pattern on the crown is variable, also. Normally, the cranial canals of the two sides are connected across the back of the head by a cross-canal known as the aural.[1] But the aural is interrupted, midway, both on one of our specimens of *pacifica* (see Garman, 1904, Pl. 2, fig. 1) and on our 457 mm. female of *atlantica*, with its two parts overlapping. And one of the large males of *atlantica* shows a still more aberrant state, with the left-hand cranial canal recurving forward toward the mid line of the head to end blind, with the aural canal interrupted (Fig. 6*C*). The large pores, also, on the sides of the head, vary in number, not only from specimen to specimen, but between the two sides of the head on some specimens. A count of 13 below the cranial canal on the left-hand side of the head of our largest male *atlantica*, in the region between eye and frontal tenaculum, but of 10 on the right-hand side, may serve as an illustration. The presence of a few sharp denticles on the mid line of the back between second dorsal fin and caudal, also on the nape, on an *atlantica* so small (151 mm. long) as evidently to have been hatched recently, deserves mention, also.

Rhinochimaera atlantica resembles its relative *Harriotta raleighana* so closely in general appearance that the one might be mistaken for the other on cursory examination, especially since the two are likely to be taken together in trawl hauls at appropriate depths on the slope, as happened on "Cap'n Bill II"

[1] Nomenclature according to Garman (1888, Pls. 1, 2, 4) and Bigelow and Schroeder (1953, p. 530, Fig. 119).

on four occasions off southwestern Nova Scotia. But it is easy to tell partly grown specimens apart, on closer inspection. Thus the glossy smoothness of the dental plates of *Rhinochimaera* con-

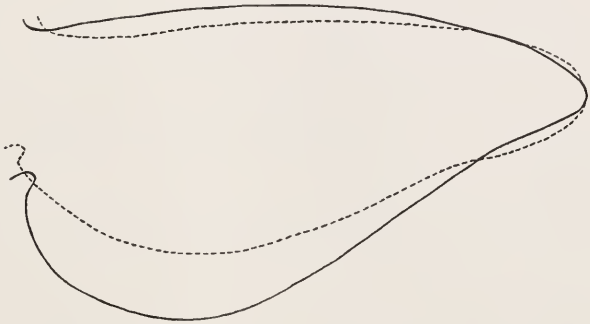

Fig. 7. Tracings of pectoral fins, adjusted to equal lengths along outer margin, to show difference in shape; solid line, *Harriotta raleighana*, female about 908 mm. long to upper termination of caudal fin, M.C.Z. No. 37726; broken line, *Rhinochimaera atlantica*, female about 1282 mm. to upper termination of caudal fin, M.C.Z. No. 37735.

trasts strongly with the grinding ridges and knobs that develop on the dental plates of *Harriotta*, soon after hatching; also, the eyes of *Rhinochimaera* are noticeably smaller than those of *Harriotta* at all stages in growth as appears from the following comparative table:

Species	Length, to termination of upper caudal[1] mm.	Sex	Ratio, horizontal diameter of eye to distance eye to base of dorsal spine
Rhinochimaera atlantica	1034	♂	1.0 : 2.80
	1130	♂	1.0 : 2.66
	1184	♀	1.0 : 3.17
	1282	♀	1.0 : 2.43
	1290	♀	1.0 : 3.03
	1295	♀	1.0 : 3.07
Harriotta raleighana	283	♀	1.0 : 1.78
	447	♂	1.0 : 1.65
	758	♂	1.0 : 1.63
	840	♀	1.0 : 2.00
	885	♀	1.0 : 1.85
	908	♀	1.0 : 2.13

[1] Approximate measurement

The pectoral fins are noticeably narrower toward the base in *Rhinochimaera* than in *Harriotta* but with more broadly rounded tip (Fig. 7). The rear edges of the dorsal fin-spine, which are serrate in small specimens of both fish, and are serrate to maturity in *Harriotta,* are perfectly smooth on large examples of *Rhinochimaera,* male as well as female. And the lateral mucous canal, which runs nearly straight rearward from its point of departure from the occipital canal in *Rhinochimaera,* or slopes slightly downward (Fig. 5*A*), bows upward at first, then turns downward — rearward in *Harriotta.*

More conspicuous differences between specimens of the two fish that are nearing sexual maturity are that the upper margin of the caudal fin thickens in *Rhinochimaera,* while developing a row of prominent denticulate structures in the males (also in some females), but with the tip of the snout continuing smooth and soft, whereas in *Harriotta* the upper caudal continues thin and smooth-edged in both sexes, but the tip of the snout stiffens in the males (not in females), bends upward, and develops a double series of rounded knobs.

It is probable that *R. atlantica* is more widespread and more plentiful in the eastern side of the Atlantic than the paucity of the previous records (one adult specimen and a few egg cases from the Irish Atlantic slope) might suggest, for this is certainly the case in the west, where "Cap'n Bill II" took it at 6 stations off southwestern Nova Scotia, at 1 station on the slope of Georges Bank, and at 1 station in the offing of New York. A table follows of localities, depths, and number, size and sex of the specimens:

Length to termination of upper caudal[1]	Total length	Sex	Lat. N.	Long. W.	Depth in fathoms	Date
151[2]	151	♂	42°22′	64°55′	290-340	7/15/53
436	457	♀	42°40′	63°51′	465-480	7/26/52
1034	1060	♂	38°52′	72°51′	415-440	6/27/53
1130[2]	1130	♂	42°40′	63°54′	520-545	7/12/53
1184	1202	♀	40°07′	68°30′	420-480	7/13/52
1282	1315	♀	42°14′	65°10′	490-530	7/28/52
1290	1315	♀	40°11′	68°16′	480-490	7/14/52
1295	1315	♀	42°38′	64°10′	460-475	7/13/53

[1] Approximate measurement
[2] Filament lost

It seems that *Rhinochimaera* is considerably less plentiful than *Harriotta* off Nova Scotia and off New England judging from the fact that four times as many specimens of *Harriotta* (32) as of *Rhinochimaera* (8) were taken by "Cap'n Bill II."

Harriotta raleighana Goode and Bean 1895

Nine specimens of this long-nosed chimaeroid had been reported previously from the western side of the Atlantic, from the trawlings made by the "Albatross" in the 1880's (Goode and Bean, 1895, p. 33), by the Prince of Monaco in 1913 (Roule and Angel, 1933, p. 75) and by "Caryn" of the Woods Hole Oceanographic Institution in 1949 (Bigelow and Schroeder, 1953, pp. 551, 552) at localities scattered along the continental slope from the offing of Chesapeake Bay to the offing of Halifax, Nova Scotia. Three specimens, also, were taken in the eastern side of the Atlantic by the "Michael Sars" in 1910 (Koefoed, 1927, p. 29), one of them near the Canaries, the other two west of Scotland. We can now report the capture, by "Cap'n Bill II," of 26 specimens of both sexes in 1952, and of 6 more in 1953, ranging from partly grown to adults.

Specimens of *Harriotta* taken by "Caryn" in 1949, and by "Cap'n Bill II" in 1952 and 1953, arranged in latitudinal sequence, south to north

Lat. N.	Long. W.	Depth fath.	Date	No.	Sex	Length in mm. to termination of upper caudal[1]	Length in mm. to tip of filament
38°43′	72°56′	630-675	June 30, 1953	1	♀	256	329
39°49′	70°05′	710-730	July 28, 1953	1	♂	375	456
40°07′	68°30′	420-480	July 13, 1952	1	♀	850	900
40°10′	68°16′	490	July 14, 1952	3	♂	702-748	742-837
41°25′	65°54′	415-490	June 19, 1949	2	♂ ♀	126-730	155-770
42°14′	65°10′	490-530	July 28, 1952	5	♂ ♀	157-447	283-550
42°16′	65°08′	370-420	July 28, 1952	2	♀	885-925	946[2]
42°22′	64°55′	290-340	July 15, 1953	1	♀	840	948
42°38′	64°04′	440-460	June 17, 1949	1	♂	735	773
42°38′	64°10′	460-475	July 13, 1953	1	♂	758	836
42°39′	63°58′	520	July 26, 1952	5	♂ ♀	283-756	373-870
42°39′	64°00′	610-625	July 12, 1953	1	♀	865	1025
42°40′	63°51′	465-480	July 26, 1952	3	♂ ♀	188-716	249-792
42°40′	63°54′	520-545	July 12, 1953	1	♂	?	775
42°40′	64°00′	440-450	June 17, 1949	1	♂	705	818
42°41′	63°49′	465-480	July 26, 1952	4	♂	250-721	295-815
42°41′	64°02′	385-400	July 27, 1952	3	♂ ♀	741-908	832-935

[1] Approximate measurement
[2] Tail lost on 925 mm. specimen

The fact that 30 of the total of 36 specimens were taken in the offing of southwestern Nova Scotia, and that 6 of the 12 successful hauls that were made there in 1952, at the appropriate depths, yielded *Harriotta*, shows that this chimaeroid is more plentiful along this part of the slope than earlier records for it might have suggested. The proportion of hauls yielding it in this region was somewhat lower in 1953 (4 out of a total of 10), though the trawlings of that summer seem to have been equally successful in general, to judge from the catches of fishes of other kinds. It appears to be less plentiful to the westward of longitude about 66°W than to the eastward, for "Cap'n Bill II" took it in only 4 hauls (6 specimens) along the slope of Georges Bank, and to the westward, out of a total of 41 hauls that she made there at 400 to 730 fathoms, in the summers of 1952 and 1953 combined.

On the Nova Scotian slope the upper limit to the regular occurrence of *Harriotta* appears to lie at about 400 fathoms although a few specimens were taken as shoal at about 340 fathoms. "Cap'n Bill II" took *raleighana* down to 710-730 fathoms, the Prince of Monaco at 728 fathoms (1332 meters, Roule and Angel, 1933, p. 75), the "Albatross" trawled it at 1081 fathoms off Marthas Vineyard, at 991 fathoms off New York, at 707 fathoms off New Jersey and at 781 fathoms off Chesapeake Bay. Depth records for it in the eastern Atlantic are 1014 fathoms (1853 meters) west of Scotland, and 1423 fathoms (2603 meters) near the Canaries (Koefoed, 1927, p. 29).

The external aspect of *H. raleighana* has been made well known by the successive studies of Goode and Bean (1895, p. 32), Koefoed (1927, p. 29), Roule and Angel (1933, p. 75), and Bigelow and Schroeder (1953, p. 551). Examination of the "Cap'n Bill II" series adds the following details.

A — Dermal denticles and dorsal fin-spine. No trace of the juvenile dermal denticles is to be seen (or felt) on specimens more than about 485 mm. long to the rearmost visible rays of the upper side of the caudal fin. A female of 300 mm. (measured similarly), still has one pair of supra-oculars, one pair on the midline of the back in the space between the first and second dorsal fins, and 4 pairs between the second dorsal and the caudal.

The increase in the size of the dorsal fin-spine with growth is not accompanied by a corresponding increase in the size of the

serrations along the rear margin of the spine, hence the latter does not feel any rougher, to the touch, on large specimens than on those of medium size. And the serrations may be partly obliterated by maturity, on some individuals, perhaps wholly so. The "Cap'n Bill II" series also verify earlier accounts of the spine as free from the margin of the fin along at least its outer half. This contrasts with the condition in *Rhinochimaera atlantica,* where the spine is smooth edged from a very early stage in growth, and where it is attached to the fin-margin, right out to its tip, or nearly so (p. 76).

B — Caudal filament. When intact, the caudal filament may be as much as 33-44 per cent as long as from snout to last visible caudal fin-ray among the smaller specimens (191-263 mm., total length). On three of our larger males (680-750 mm., total length) the filament is 111-116 mm. long, and 160 mm. on our largest female (1025 mm., total length). But it is so thread-like toward its tip that there is always a possibility that part of it may have been lost, even on specimens on which it seems to be intact.

C — Pattern of mucous canals on head. Cumulative evidence is conclusive, that the pattern of mucous canals on the head varies too widely to have much significance in taxonomy, not only between different individuals, but even between the two sides of the head of a single individual in many cases. On three of the larger males, for example, the jugular canal and the oral diverge jointly from the orbital canal on one side of the head, but separately on the other side with an interspace between them (Fig. 6*D, E*). When they arise jointly they may separate at once or they may run for a longer distance or a shorter as a joint trunk before they diverge, one from the other. On one specimen of each sex the jugular canal fails to connect with the orbital on either side of the head, while on one male it ends blind on the right-hand side but connects with the orbital on the left-hand side.

D — Snout, and sexual tenacula. In *H. raleighana* the snouts of the males are similar to those of the females, up to a length of 450 mm. or so (to last visible caudal rays); and no trace is to be seen of the frontal tenaculum, or of the prepelvic tenacula, although the prepelvic pockets are already formed on newly hatched specimens. But the tip of the snout has begun to curve

upward, its terminal knobs have formed, the sexual tenacula have developed in the males, and the claspers seem to be ready to function by the time a length of about 650 mm. (to last caudal rays) has been reached.

The largest male yet recorded is about 836 mm. in total length (758 mm. to last visible caudal ray). A female 990 mm. in total length including a caudal filament of about 125 mm. as scaled from Roule and Angel's (1933, Pl. 4, figs. 34-34a) illustration, and another 1025 mm. in total length, including caudal filament of 160 mm. (Cap'n Bill II'' specimen) are the largest yet seen of that sex.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3

STATUS OF INVERTEBRATE PALEONTOLOGY, 1953

Bernhard Kummel, *Editor*

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
October, 1954

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 112.

Breviora (octavo) 1952 — No. 35 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 33 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 17 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

These publications issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

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No. 3. Status of Invertebrate Paleontology, 1953

Bernhard Kummel, *Editor*

Documentation and interpretation of data on fossil invertebrates have actively engaged many scientists for more than a hundred years. The historical development and methods of documentation can be divided into four phases. (a) Description of the faunas of a region; Sowerby's Mineral Conchology and d'Orbigny's Paléontologie Francaise are classic examples of this type. (b) Monographs of zoological groups by stratigraphic horizons. (c) Extensive monographs of animal lineages through all or part of their history. (d) Condensed works or phylogenies covering whole classes or phyla. Needless to say, contributions falling in categories (a) and (b) are primarily documentary, hence must occupy much of the attention of our profession. All interpretation of fossil invertebrates must ultimately stem from this type of work. Contributions in categories (c) and (d) are fewer in number and more difficult to attain. It is in these broad syntheses that we seek ultimate meaning in paleozoology, evolution, and geologic history.

Great advances in recent years in genetics and neontology have broadened understanding of population structures, processes of isolation, and intraspecific variation. Whereas the paleontologist can contribute little towards the understanding of the mechanism of evolution, he can and does contribute the dimension of time and thus supplies substantial evidence for the interpretation of evolutionary patterns. Current taxonomic arrangements of the invertebrates have been built up by many individual specialists working generally with small and geologically restricted groups.

The projected Treatise on Invertebrate Paleontology under the editorship of Raymond C. Moore represents the largest organized effort in the history of our science to summarize knowledge of fossil invertebrate animals. The Treatise will contain data on the morphology, systematics, and evolution of all of the invertebrate phyla known to paleontology, and it will provide a substantial foundation for further advances.

The purpose of the present symposium is to assess in broad perspective the status of invertebrate paleontology. It brings together specialists who will present thumb-nail summaries on the

status and problems of taxonomy, evolutionary patterns, and geologic history of many of the invertebrate phyla, especially for the non-specialist. The total sum of these contributions is a partial review of current thought and interpretation of fossil invertebrates.

These papers were presented orally at the annual meeting of The Paleontological Society in Toronto, Canada, November 10, 11, 1953.

Symposium Committee
J. Wyatt Durham
N. D. Newell
B. Kummel, *Chairman*

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

I. *Toward a More Ample Invertebrate Paleontology*

By Norman D. Newell

The American Museum of Natural History
and Columbia University, New York

It is essential in any assessment of invertebrate paleontology to keep in mind that it originated, and to a large extent has developed, as a stratigraphic tool. In North America, particularly, we have tended to be concerned with the *uses* of invertebrate fossils in the solution of geologic problems rather than with the *meaning*, in the broadest sense, of the fossils. The emphasis has been that of an applied rather than a pure science. Let it be granted that the discovery of the useful attributes of fossils forms one of the grand chapters in the early history of geology, leading directly to the chronological classification of the geological record and all that this implies in the story of life. Although this is, indeed, a tremendous contribution to human knowledge, there is much more to be learned from fossils.

Fossil invertebrates, because of their ubiquity, convenient size, and relative ease of recognition, have always been favored over other fossils by field geologists, and it is not surprising that the study of their distribution has become an essential part of stratigraphy. Without the data from these fossils our knowledge of the details of geologic succession, correlation, and past geographies would indeed be very sketchy. The debt which stratigraphic geology owes to paleontology, especially invertebrate paleontology, is great, and the debt which paleontology owes to stratigraphy is equally great. However, it is too often implied that chronology is the chief or the only contribution to human knowledge that our science can make. Nothing can be farther from the truth.

The scope of our subject is vast, covering the enumeration, history, distribution and ecology of a score of animal phyla and a hundred or so orders, many of which have not yet really been subjected to intensive inquiry. The literature is diffuse and the numbers of genera are legion. Since the total number of investiga-

tors is woefully inadequate as compared with the size of the task, there has inevitably been a tendency toward extreme specialization along taxonomic, stratigraphic, and even provincial lines. Under the circumstances, our work has not, in general, been characterized by broad syntheses.

There are, however, many signs that we have begun the ascent from an intellectual plateau in our subject since the second World War. Increasing effort to sharpen the utility of fossil invertebrates as stratigraphic guides is leading competent investigators to recognize some of the blind alleys where the labors are not rewarded by commensurate returns. Many are beginning to attack problems of broader significance. In the development of commercial micropaleontology by the petroleum industry, we very probably are witnessing the final stage in maturing of theories of paleontologic correlation. The continuous growth of knowledge in this subject has not resulted in revolutionary new developments since the general recognition of the importance of biologic facies. Increasing numbers of stratigraphers are impressed by the fact that stratigraphic relationships of separate outcrops within a sedimentary basin are sometimes more readily determined by simple tracing and matching of strata than by comparison of suites of fossils. Many of these investigators are giving more attention to fossils as indicators of environment, a field rich in unexploited possibilities. In many cases the evolutionary changes within a fauna during deposition of a stratigraphic sequence are so slight that for all practical considerations the fauna ranges without appreciable change from bottom to top of a succession. The application of statistical methods in the analysis of such a faunal sequence promises to permit further refinement of paleontological zonation. However, in a majority of cases successive modifications induced by shifting environment may be more conspicuous than changes resulting from evolution. Although statistical methods will certainly aid in the recognition of subspecies and in study of obscure trends, the evaluation of these trends, of course, must remain largely subjective. Mathematical treatment of fossils does not offer a general solution of our problems.

Occasionally the field geologist, on submitting his collection of fossils to the paleontologist for study, is disappointed because

the material fails to elicit the desired information as to geologic age. It may be that the collection is poorly preserved or fragmentary or, more commonly, the most distinctive guide fossils are lacking in the material. This may seem to reflect on the competence of the paleontologist or to cast doubt on the whole principle of paleontologic zonation. In very many cases the geologist in search of refinement of zonation of a stratigraphic sequence makes demands that cannot be satisfied by the materials at hand. So-called facies fossils, on the other hand, may lead to valuable inferences with respect to past environments. We suspect that often the wrong answers are sought from the materials at hand.

If the signs of change in emphasis are correctly read, I venture to prophesy that developments in invertebrate paleontology during the next few years will be characterized by increasing emphasis on the more biological aspects of invertebrate paleontology. Even now, it is hardly appropriate to describe paleontology as the "hand-maiden of geology". Its role in earth sciences is at least as significant as those of petrology or structural geology,

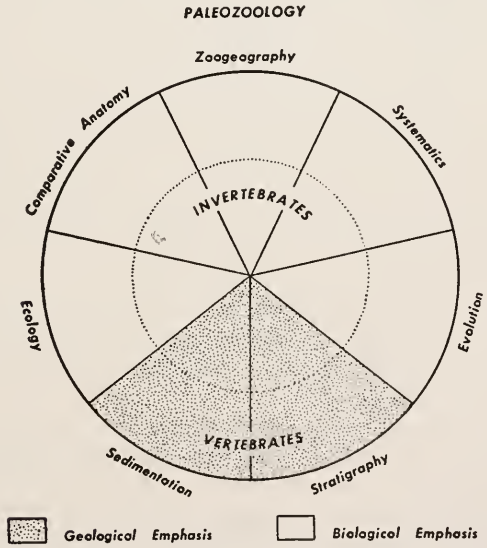

Fig. 1. Biological and physical aspects of paleozoology.

neither of which is primarily esteemed for useful applications to other disciplines.

Paleontology is constituted of diverse matters (Fig. 1) many of which have little to do with geologic problems, *per se*. Evolution, ecology, systematics, comparative anatomy, and zoogeography of fossil invertebrates offer a wide range of fields of investigation outside the usual scope of stratigraphic geology. Geology can and does benefit from the more biological branches of paleontology; and, *of course*, the stratigraphic aspects of paleontology are absolutely fundamental for the establishment of chronological sequence and correlation in the history of life; but balance must be sought in the application of our energies if we are to achieve the most complete understanding of the history of life on earth. The biological aspects of invertebrate paleontology, which have not received as much attention as the physical aspects, now offer the greatest opportunities for investigation. By general agreement, paleontology is a full member of the family of earth sciences. It must be stressed, however, that it really involves much more of biological than physical sciences.

Tangible evidence of a strong trend in our profession toward a general broadening of the field of interest is manifest in two great group projects of incalculable importance to invertebrate paleontology. They involve active collaboration of more than 150 investigators. They are: The Treatise on Marine Ecology and Paleoecology under the leadership of Harry S. Ladd, and The Treatise of Invertebrate Paleontology under the leadership of Raymond C. Moore. These two modern syntheses will open new vistas to students of invertebrate paleontology. They will provide inspiration and rich sources of information in the quest for a broader understanding of fossil invertebrates.

We are in the midst of a new flowering of interest in organic evolution in which genetics, systematics, and paleontology join hands, and the vitality of this movement is making a deep impression on our own science.

In these notable efforts we see evidence of a gradual widening of appreciation and interest in many of the fundamental problems of invertebrate paleontology. These are exciting developments in which attention is increasingly focused on the fact that fossils are the remains of organisms rather than being simply

stratigraphic tools. The new emphasis inevitably will lead to a more ample science. The symposium of The Paleontological Society, planned and organized by Dr. Bernhard Kummel, clearly indicates interest in the fundamental problems of our science.

If we must limit our attention to the strictly "practical" points of view, many fundamental problems of paleontology may seem utterly esoteric. Many of us, however, give at least lip service to the thesis that pure science is also intensely practical. "The whole of man's experience has demonstrated that the practical results required for tomorrow depend essentially on the 'impractical' free curiosity of today." The broad problems of paleontology are important to us, if I may paraphrase Warren Weaver (1953), because they have "depth and sweep, because they are esthetically attractive, because they are instances of man's mind seeking to meet the challenge of the universe."

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953

II. *Protozoa*

By Hans E. Thalmann
Stanford University, Stanford, California

In the field of fossil Protozoa great advances have been achieved during the past hundred years. At that time it was relatively easy for a paleontologist to overlook, singly, the different branches of the modern science of micropaleontology. Today even a specialist will have to devote his time either to a single class of microfossils or, as is more often the case, to a selected group within this class. The doctrine of mechanism, Darwin's ideas on natural selection and organic evolution, improvement of optical instruments from the simple microscope to the modern electron-microscope, refinement of methods and techniques and last, but not least, the paleontologist's incurable curiosity to penetrate deeper into the secrets of Nature, have contributed to the accumulation of knowledge of the most primitive forms of life buried in sediments since pre-Cambrian time. Truly enough, we are not yet standing on top of the pyramid of knowledge, but each new contribution adds another stone that broadens the foundation on which we build up understandingly and intelligently the science of fossil Protozoa, by unraveling their geologic history, their trend of evolution and phylogenetic relationships, and by solving the problems of paleoecology and paleogeography.

In the following pages an attempt is made to summarize the *status quo* of our knowledge of the fossil Protozoa. The limited space available for such a thumb-nail summary does not permit one to give full credit to the legion of authors to whom every paleontologist is indebted for his contributions, small or large.

Phytomonadina. So far only one representative, *Chlamydomonas,* is known from the Upper Eocene, plus *Phacotus* which is known from the Upper Miocene and forms limestones in the Pleistocene, thanks to its calcareous tegument.

Xanthomonadina. Although forming siliceous cysts, this group

is not yet definitely known as fossil. With the help of modern optical instruments, however, there is every possibility that they might turn up when searched for in bituminous deposits.

Euglenida. *Phacus* and *Lepocinclis* are known from bituminous sediments of Eocene age, and *Trachelomonas* has been found in the same habitat of Pliocene age.

Dinoflagellata. Great progress has been made during the last two decades thanks to the intensive research work by G. Deflandre and O. Wetzel. Nearly half a hundred genera, three-quarters of which are exclusively fossil, are presently known, most of them organically conserved thanks to the fossilization of their cellulose thecae. They are now traced back to the Jurassic, but their phylogenetic relationships are still only vaguely known. The question of whether the siliceous Dinoflagellata might be ancestral to the Radiolaria, and the calcareous Dinoflagellata to the Foraminifera, is not yet settled.

Ebriidea. These marine planktonic flagellates with siliceous endoskeleton have only recently become known as fossils, appearing suddenly in the lower Tertiary. They are already represented by about 20 genera, and more representatives are likely to be found in pre-Tertiary beds with the help of modern optical instruments and more refined techniques.

Silicoflagellata. Relatively little progress has been made in silicoflagellate research. It is an open field for investigation, and the question, whether animal or plant, has not been settled. These marine flagellates with siliceous tests of only a few microns are known since Middle Cretaceous. Curiously enough, fossil Silicoflagellata are at present better known than the Recent ones, and definitely show evolutionary tendencies from geologically older to younger forms. Recent work by G. D. Hanna and Y. T. Mandra, although concerned only with a few Californian sediments already indicates that the Silicoflagellata might have future use as stratigraphic tools and ecologic indicators.

Coccolithophoridea. Although known as fossils since Ehrenberg (1836), the true nature of these extremely minute, rock-forming, planktonic, calcareous flagellates (''coccospheres'' or ''coccoliths'') was only recognized about 50 years ago by Lohmann (1902). They still are obscure as to their origin, appearing since Liassic time, but modern research work with the help of

the polarization- and electron-microscope will certainly enhance our knowledge of this class of Protozoa, which today are grouped into the orders of Heliolithae (3 families with 25 genera), and Ortholithae (3 families with 6 genera). Recent studies indicate their possible stratigraphic value. Some "Problematica": *Ceratolithus* Kamptner, *Nannoconus* Kamptner, *Lithostromatium* Deflandre and *Peritrachelina* Deflandre, all about 12-20 microns, are still not taxonomically pigeon-holed (Flagellata *incertae sedis*).

Chrysomonadina. Formerly assigned to the *Coccolithophoridea,* they are now separated as a distinct group. Minute siliceous cysts belonging to *Archaesphaeridium* Deflandre and *Micrampulla* G. D. Hanna are known from Cretaceous beds, others from Eocene lignites, Miocene fresh-water diatomites and Pleistocene peats. The taxonomic position of *Palaeostomocystis* Deflandre, a planktonic flagellate in Jurassic and Cretaceous beds is not yet settled.

Chitinozoa. Discovered in insoluble residues of Ordovician and Silurian limestones by Eisenack, the Chitinozoa are also of unknown systematic position. Their youngest representatives so far are reported from the Middle Devonian but more intensive studies are necessary before their true nature and taxonomic place are fully understood.

Thecamoebina. Fossil Thecamoebina have been reported to occur in Middle Eocene deposits, but recent studies by Bolli and Saunders (1954) indicate that most, if not all, so-called fossil forms might in fact be Recent representatives, often erroneously attributed to the Foraminifera. Similarity between tests of Thecamoebina and certain genera of the Saccamminidae (Foraminifera) seems to be responsible for this error. The presence of thecamoebian forms as "fossils" apparently is due to contamination from fresh-water rivers, lakes and swamps. "Fossil" representatives of the "foraminiferal" genera *Leptodermella* and *Milletella* should now be allocated to the Recent thecamoebian *Centropyxis, Lagunculina* and *Urnulina* to *Difflugia,* and some species of *Proteonina* to either *Pontigulasia* or *Difflugia.* Bolli and Saunders' studies rule out the Thecamoebina as fossils.

Tintinnoidea (*Calpionellidae*). Great progress has been made in the recognition of the true systematic position of these lori-

cated oligotrichous Infusoria, which as planktonic microfossils were populating the seas during Upper Jurassic and Lower Cretaceous. G. Colom (1948) has excellently summarised our present knowledge of these tiny marine, pelagic and free-swimming, therefore widely distributed, organisms of the old Tethys region. They suddenly appear at the base of the Tithonian and persist as rock-formers associated with *Nannoconus,* coccoliths, and radiolarians, into the Barremian where they abruptly disappear. Their presence in sublithographic limestones, where the calcified loricae appear brightly white in a dense grey groundmass, indicates a warm tropical environment. Few, if any, fossil tintinnoids have been reported from the Western Hemisphere but a search for them in beds of Jurasso-Cretaceous age will undoubtedly reveal their presence and might help to correlate dense sublithographic limestones when megafossils or Foraminifera are scarce or absent.

Radiolaria. The taxonomy of the Radiolaria, based on the composition of their siliceous skeleton, has recently been summarized by A. S. Campbell (1952). These wonderful microscopic animals of the seas have for a hundred years been the object of study for their beauty and multiformity, although still practically nothing is known regarding the formation of the test in these sarcodine Rhizopoda. For the geologist and paleontologist there are only two of the four groups of Radiolaria regarded as fossils of importance, the peripylean Spumellina and the monopylean Nassellina, occurring as microfossils in all types of siliceous rocks from Cambrian to Recent all the world over. Their exclusively marine planktonic mode of life, although passively transported by currents, is responsible for their world-wide distribution, from littoral to deep-sea sediments. They are excellent indicators of paleoecological conditions if and when properly evaluated. Their stratigraphic use is at present confined to local correlations, but further research indicates that many radiolarian genera and species might become good guide-fossils and help out, as in the case of calpionellids and coccolithophorids, when megafossils or other microfossils are absent or of little value.

Foraminifera. Without any doubt the greatest advances made in the study of fossil Protozoa have been made in the order of the Foraminifera during the last hundred years or so. This prog-

ress is evident when d'Orbigny's classification of 1852 is compared with the modern taxonomic treatment of the testaceous rhizopods in the modern handbooks of Galloway (1933), Glaessner (1945), Cushman (1948), and Sigal (1952).

Sigal's and Glaessner's classification seems at present to be the most comprehensive and logical one, grouping the order of Foraminifera conveniently into three suborders: the Uniloculinidea (gelatinous, chitinous or slightly agglutinated tests, not yet found fossil), the Biloculinidea (globular proloculus followed by a tubular chamber), and the Pluriloculinidea (uni- or pluriocular proloculus followed immediately by a series of simple or complicated chambers). These three suborders include seven superfamilies with altogether 61 families and many subfamilies comprising approximately 1200 valid genera and subgenera — thus contrasting strikingly with the seven "orders", few families and less than 100 genera of d'Orbigny in 1852. The tendency in modern foraminiferal taxonomy is overwhelmingly in the direction of a natural classification. For such an end the Foraminifera are excellently suited, thanks to their abundance in all sediments of the geological column which allows morphogenetic and phylogenetic studies of their evolutionary pattern and geologic distribution. It has to be admitted, however, that the ultimate goal in every branch of paleontology has not yet been reached in the Foraminifera: a true natural classification. But at least one important principle is now settled, namely, that the primitive forms were non-septate, and thus precede geologically as well as phylogenetically the cohorts of septate, and especially septate-spirally-coiled, more highly developed forms.

Much research work will have to be done with regard to the more complex families in order to understand their phylogenetic relationships. This is evident in Hofker's new attempt at a natural classification (1951), that is by using micro-anatomical studies of the tiny tests in order to establish the phylogenetic concatenation of the genera and families of Foraminifera, fossil and Recent. In establishing true natural relationships it is of utmost importance, according to Hofker, to study and follow in time sequence, the nature and behavior of the dentate buccal apparatus or "toothplate" and its connection either with the protoforamen or with the deuteroforamen in the chambers of

the foraminiferal test, and the pattern and distribution of the pores in the test-walls. Glaessner (1954) has summarized the new aspect of foraminiferal morphology and taxonomy initiated and so strongly advocated by Hofker. Studies by Arnold (1954) on the evolution of the Foraminifera, stressing their variation and isomorphism, will also shed new light on taxonomy of the group, as will Wood's (1948) interesting investigations of the structure of the wall of the foraminiferal test. A new field of study is now opened with the use of the electron-microscope where magnifications up to 4000 times reveal highly interesting morphological characters (Jahn, 1953).

The principle of phylo-morphogenetic analysis, initiated by the late Tan Sin Hok on *Cycloclypeus* and other larger Foraminifera, is gaining more and more ground leading to many hitherto unsuspected genetic relationships in different groups of smaller and larger Foraminifera, and will become increasingly more important for stratigraphic correlation purposes. The abundance of material for such studies and for biometrical analysis, and the relatively easy technical preparation of it, is hardly surpassed by any other group of fossils.

The geologic history of the Foraminifera dates from the Cambrian. Presence of calcareous forms in Cambrian time has now definitely been disproved, and it is not before the beginning of Middle Devonian that the first calcareous genera appear. The Lower Paleozoic is the time of the arenaceous genera and species (Ordovician, Silurian and Devonian). With the sudden evolution and development of the calcareo-arenaceous endothyroids and fusulinids at the end of the Mississippian and throughout the Pennsylvanian, the development of calcareous perforate tests in Foraminifera increases rapidly, especially when the Triassic-Jurassic boundary is reached; here more than half of the families of Foraminifera have their origin, and persist, with few exceptions (Orbitolinidae, Spirocyclinidae, Stomiosphaeridae, Gümbelinidae, Meandropsinidae, Hantkeninidae, Orbitoididae, Discocyclinidae, Victoriellidae and Miogypsinidae) to Recent time.

The spectacular explosive and sudden evolution and development of the rock-forming Fusulinidae during Pennsylvanian and Permian, and their complete extinction at the end of the Permian is a unique feature of the younger Paleozoic, repeated again, to a

lesser degree, by the Alveolinidae during Upper Cretaceous to Oligocene times, the Orbitolinidae during Cretaceous, the Orbitoididae from Upper Cretaceous to Miocene, the Discocyclinidae during Eocene, and the Nummulitidae during the Paleogene.

Wide lacunae of knowledge of the Foraminifera (excepting Fusulinidae) still exist generally for the whole of the Paleozoic, Triassic, Jurassic and Lower Cretaceous periods. Many of the pluriloculinid families have their roots in either Triassic or Jurassic beds and unless we can learn more about the assemblages and faunal composition of these periods the phylogeny of the Foraminifera will remain incomplete. The large families of Lagenidae and Rotaliidae play an important role during the older Mesozoic, aside from some prominent arenaceous families, and many ancestral genera will still have to be detected in years to come. Future foraminiferal studies will have to emphasize the importance of the Lower Paleozoic and Lower Mesozoic Foraminifera, and it is a healthy sign that recent monographs are devoted, in increasing numbers, to these so-far neglected faunas.

Since a great share of the total crude oil production in the world is found in Upper Cretaceous and Tertiary formations, much more attention has been paid to the foraminiferal assemblages of these beds in practically every country where oil wells are drilled or exploration for hydrocarbons is under way. Much more is, therefore, known about smaller and larger Foraminifera (except for the Paleozoic Fusulinidae) of the last sixty or seventy millions of years in our geologic history than of the preceding five hundred millions. During the Cretaceous the important planktonic Foraminifera, especially Globigerinidae, appear and these widely distributed "Ammonites of the Tertiary" have since proved to be of enormous stratigraphic value *(Globigerina, Globorotalia, Hantkenina, Orbulina, Pseudotextularia,* etc.) for interregional and intercontinental correlation of contemporaneous beds and formations or, as is the case especially for Pliocene and Pleistocene sediments, for interpreting paleoclimatic and paleoecologic conditions. The value of orbitoids and nummulites for world-wide correlations has been known for a long time and the number of benthonic forms, as *Globotruncana, Bolivinoides, Flabellina,* certain *Rotalia* species, etc., as time-markers is ever increasing. The Globotruncanae with their short-lived and explo-

sive development are at present one of the most useful tools for world-wide stratigraphic correlation of Upper Cretaceous sediments from Cenomanian to the end of Maestrichtian.

In applied micropaleontology, nowadays, the paleoecologic significance of the Foraminifera is of great importance in reconstructing the bionomics of former habitats and, most valuable of all, in elucidating lateral and vertical facies changes in the sediments. Studies on Recent faunal assemblages in different habitats, nekrocoenosis as well as biocoenosis, demonstrate the dependance of most of the Foraminifera on varied biological factors ranging from depth and temperature, light penetration, food supply, salinity, calcium carbonate content, nutritious salts, etc. to factors regulating the rate and mode of sedimentation, nature of bottom sediments and influence of litho-facies of the embedding sediments.

In order to establish biochronological zones and paleoecological conditions, each sedimentary basin has to be studied as a unit, covering for each formation present, all facies and habitats from reef and near-shore to deep-sea environment. Only after adjoining basins have been treated similarly as a unit, will it become permissible to generalize or to make inter-basinal or inter-regional correlations and paleogeographic deductions about the individual formations. Up to now quite a few basins have been studied in such a way, and future progress in everything concerned with Foraminifera will be dependent on the amount of team work undertaken, in cooperation with specialists in other fields of paleontology, and thus shall the geologic history of the earth become fully understood and the documents which Nature provides us in the form of large and small fossils shall be intelligently deciphered. Likewise, concerted efforts of every micropaleontologist to reach and achieve a natural classification of the Foraminifera and other classes of Protozoa, and a purification of their nomenclature will be a *conditio sine qua non* for the next hundred years.

As Albert Gaudry said in 1890: . . . "nous ne devons désespérer de rien; peu à peu nous découvrirons dans les couches terrestres les ancêtres des créatures qui nous entourent, si délicates qu'elles soient."

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953

III. *Coelenterata*

By John W. Wells
Cornell University, Ithaca, N. Y.

These remarks are admittedly somewhat subjective, and some points are to be taken as stimulants to cast light in still dark places. I have divided my time amongst three aspects of coelenterate paleontology: classification, evolution, and paleoecology.

The classification (Fig. 1) as a whole is in no better shape than that of most other phyla. Even the name of the phylum is not wholly free from question. The coelenterated animals are obviously divisible into two distinct groups: (1) the Cnidaria (which most people mean when they say Coelenterata), and (2) the Ctenophora. Opinion favors recognition of two phyla (Hyman, 1940), and my comments are wholly confined to the Phylum Cnidaria, divided by tradition and on morphological grounds into three geologically ancient classes: (1) Hydrozoa, (2) Scyphozoa, and (3) Anthozoa. It is, of course, in the ranks below the classes that we find divergent ideas of classification, and the deeper we go the more we have a feeling of working our way through a dark cellar full of cobwebs, a feeling not peculiar to the Cnidaria.

In the Hydrozoa only the order (or class?) Stromatoporoidea has much of a chronological record, but rather than being thereby on firm ground, this extinct group of reef dwellers has given the most trouble at the highest systematic level. They have been claimed for the Foraminifera (Hickson, 1934; Parks, 1935), and sponges (Heinrich, 1914; Twitchell, 1929) as well as for the Cnidaria. The sum of morphological characters favors strongly a hydrozoan connection (Lecompte, 1951), but evidence of this position is largely negative, except that the fundamentally trabecular structure of the coenosteum is like unto only that of cnidarians.

The pelagic siphonophores are best left to the neontologists. Their only fossil representatives are vellelids and porpitids from

the Paleozoic (Caster, 1942), significant only as being indicative of the antiquity of this group.

The Scyphozoa, like the siphonophores, are notorious amongst paleontologists for their lack of hard parts. They appear here and there in the geologic column as stray and aggravatingly

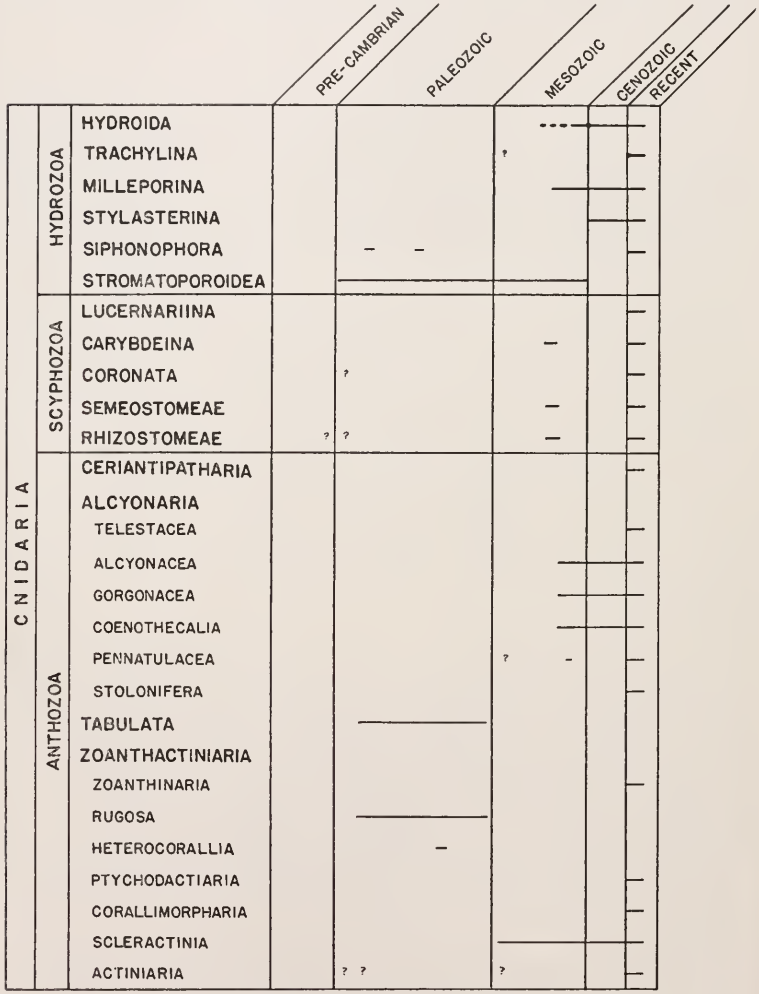

Fig. 1. Classification and chronology of the Cnidaria.

vague impressions from the Precambrian on, but the fossil material signifies little in the systematics of the jellyfish. Perhaps I may mention here the conulariids, another perplexing group, possessed of a thin, phosphatic skeleton, whose tetrameral symmetry has suggested to some workers a scyphozoan relationship. Indeed, it is hard to think that such a form as the Ordovician *Conchopeltis,* the only conulariid for which traces of the tentacles have been found, was not a jellyfish. But then, *Conchopeltis* may not have been a conulariid.

In the Anthozoa we find a really significant chronological record, and it is on the tabulate, rugose ("tetracorals"), and scleractinian ("hexacorals") corals that the most work has been done. These are all clearly anthozoan cnidarians. The scleractinians are clearly from the same stock as the corallimorph anemones rather than directly from actiniarian anemones, as indicated lately by studies of nematocysts (Carlgren, 1940, 1943, 1945). But the relations of the extinct tabulates and rugosans to skeletonless stocks are still speculative; both are cryptogenic and probably polyphyletic groups appearing first in the Ordovician without any known phyletic past.

In the corals, as in other organic groups, the systematic value of morphological characters is the chief classificatory problem. Modern classifications are, or ought to be, phylogenetic, and to discover the bases for such classifications, characters must be found which show a certain degree of constancy and which also reflect the fundamental organic plan of the animal. In the rugose and scleractinian corals these characters are to be found in the septa, which reflect the mesenteries, which in turn are the primary structures of the anthozoan polyp. The mode of insertion, development, and microstructure of the septa are thus of basic significance. This was first recognized some time since for the scleractinian corals (Pratz, 1882; Vaughan and Wells, 1943) and is now finally being found to lie at the roots of rugosan systematics (Wang, 1950; Lecompte, 1952). The structure of the septa, when more thoroughly understood than at present, will enable us to thread our way through dense overgrowth of homeomorphs, "morphic equivalents," "radicals," morphogenetic trends, and confusion due to ecologic plasticity. The tabulates have not yet revealed such constant but truly basic structures, a situation

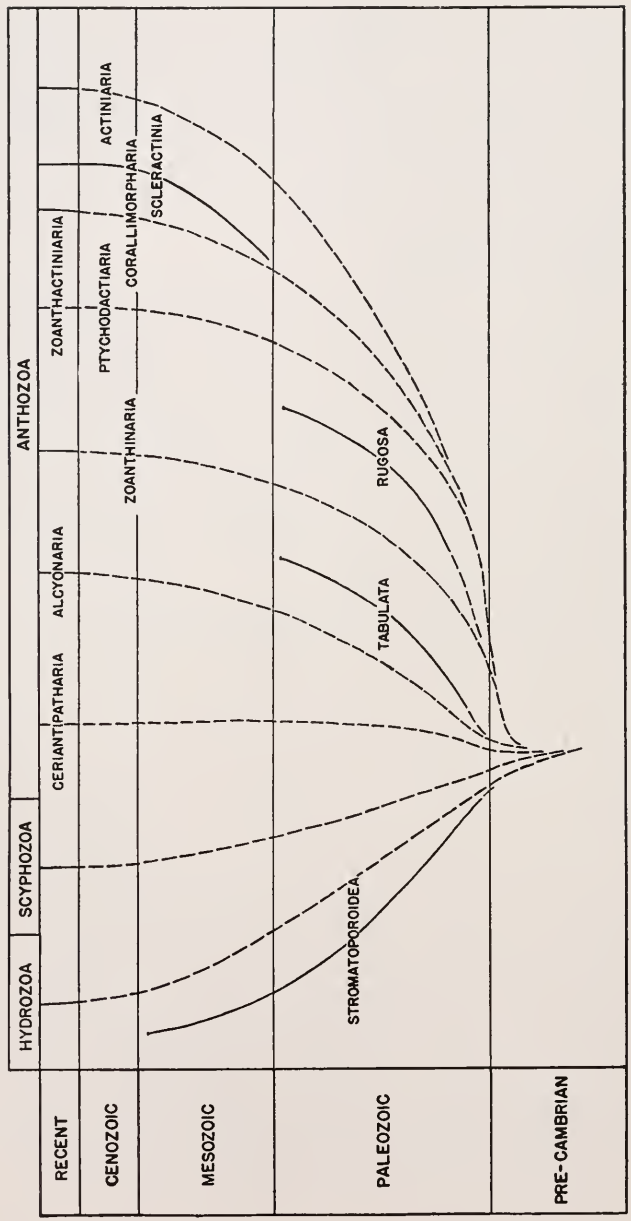

Fig. 2. Evolutionary pattern of the Cnidaria.

reflected in their chaotic systematics, wherein strongly differing forms are artificially lumped together by homeomorphy rather than phylogeny, on the feeble basis of negative characters (Lecompte, 1952). Thorough analysis of their microstructures, a very difficult task in all Paleozoic corals, should help to clear up the taxonomy of the tabulate group or groups, and may or may not sustain the often-made suggestion of a relationship with the alcyonarians (Hickson, 1924, *int. al.*).

The general evolutionary pattern of the major cnidarian groups is only hinted at in the structural series of living forms, and has found little or no actual confirmation from the fossil forms. It should be remembered that a calcareous skeleton, sometimes calcitic, sometimes aragonitic, is an evolutionary development which has appeared at different times in different cnidarian lines, each time being a secondary acquisition consequent on sedentary habits. This scattering appearance of a major structural type seems peculiar to the Cnidaria, in which it has occurred on widely-differing plans, in about half of the major groups.

As shown by Figure 2, it appears, solely from the living structural and ontogenetic series, that the hydrozoans are the most primitive cnidarians and hence presumably appeared first, that the scyphozoans came next, followed by the structurally advanced anthozoans. The fossil record does indicate, at least, that the three classes were probably differentiated by the beginning of the Cambrian. Supposed jellyfish occur in Precambrian rocks, and reputed skeletonless zoanthactiniarians are reported from the Cambrian (Clark, 1913; Dollfus, 1875). It is otherwise in the groups with a respectable paleontological record.

The evolutionary pattern of the stromatoporoids and tabulates is extremely obscure, partly because they have not really been thoroughly studied, and partly because they seem to have been remarkably self-satisfied organisms. The Milleporina and Stylasterina have as yet too few known fossil forms to allow any generalizations on their history, except that they are a relatively recent development.

Of all the cnidarian groups, only two have an abundant fossil record nearly from their first inception — the Rugosa and the Scleractinia. Only the latter is represented by any living forms,

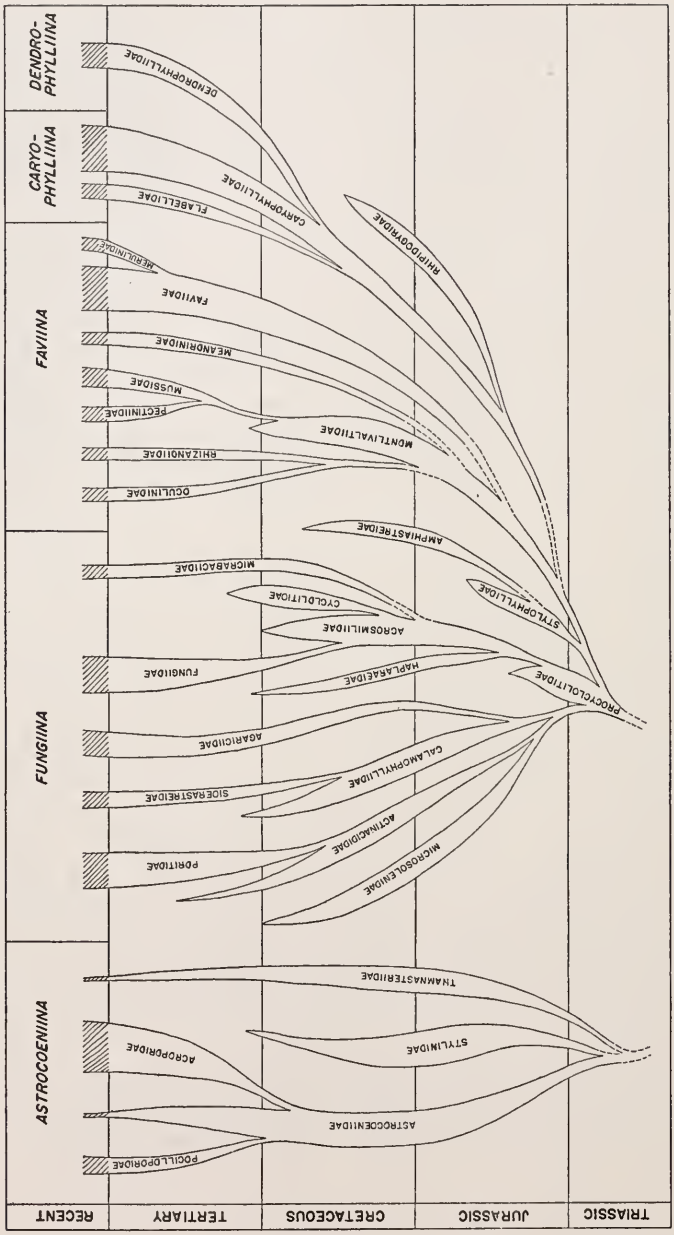

Fig. 3. Evolutionary pattern of the Scleractinia.

which is a fortunate situation, for it sheds some light on the general evolution of the other anthozoan corals. The principle which serves in the classification of the Scleractinia — that the septal structure is constant within a group and that it is progressively modified in each group, often in more than one direction with the passage of time — is also the guide to the broad evolutionary history of the group (Fig. 3). The concept of morphogenetic trends (Lang, 1917, 1923, 1938; Vaughan and Wells, 1943) also sheds light on the evolution of lesser categories, especially at the generic level. Here, while septal structures remain relatively constant, the form of the corallum changes systematically, often in several directions and on two levels (first-order and second-

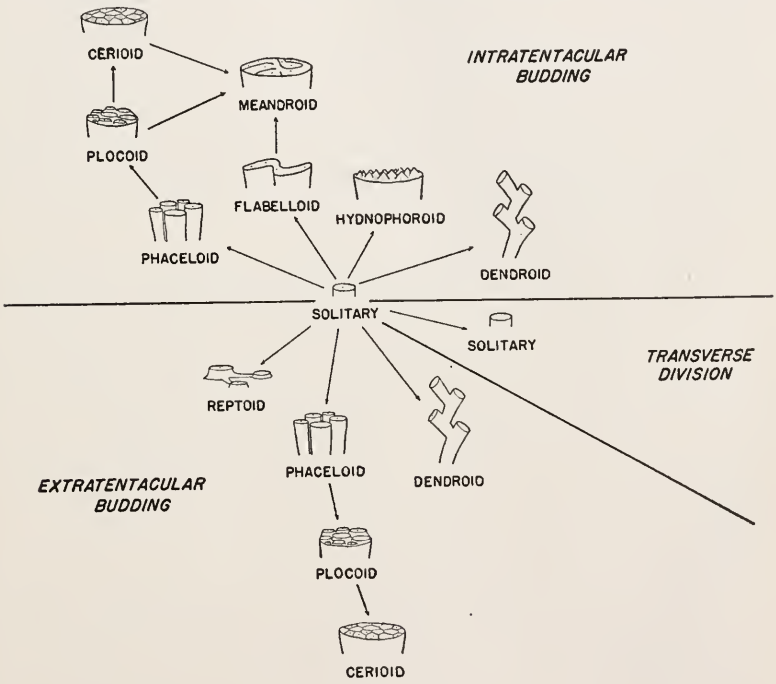

Fig. 4. First-order morphogenetic trends in scleractinian corals, conditioned by modes of colony-formation.

order trends), from solitary to colonial, from relatively simple to fairly complex colonial structures, the latter being the termination of trends from which little more than mere survival may be expected. Figure 4 shows some of the potential first-order trends in colony formation from a solitary founder polyp. But, if we add to these such seemingly genetic, second-order trends as the encrusting, massive, ramose, and foliate habits, which may operate on nearly all of the first-order forms, something like 45 distinct colonial forms are possible, and the discouraging specter of homeomorphy looms ever and ever larger. For instance, *Montlivaltia*, a common Mesozoic genus of solitary forms, now stands revealed as a monostomatous progenitor from which, by various first- and second-order trends, many homeomorphic colonial types arose at different times from different species, and many good species of *Montlivaltia* are known from the late Triassic well into the Cretaceous. At present the colonial montlivaltians are generically divided on the basis of modes of colony-formation, but it is obvious that these "genera" are no more than form-genera, and the tracing of polyphyletic developments in this subfamily alone will require very large collections, much time, and painstaking study.

One of the most debated questions in the evolution of the anthozoan corals is the relation of the scleractinians to the rugosans. It boils down to whether the scleractinians were filiated from the rugosans (Schindewolf, 1942), or whether they were independently derived from skeletonless anemone stocks: the scleractinians from the stock which led to the living corallimorphs and actiniarians (Carlgren, 1918; Stephenson, 1921), and the rugosans from earlier stocks leading to the zoanthids (Duerden, 1902, Hyman, 1940). Chronologically and to some extent ecologically, the scleractinians succeeded the rugose corals and it is tempting to see in them revivified rugosans. It would seem that the ancestral stock should be found in the late Paleozoic corals, but it is generally admitted that the rugose corals of the Permian are the specialized end-forms of a long-lived line of solitary forms (Schindewolf, 1942). To derive the Scleractinia from these, we have to assume (1) a possible change in skeletal substance from calcite to aragonite, (2) a complete change in the microstructure of the septa, and (3) a change in the mode of mesenterial and

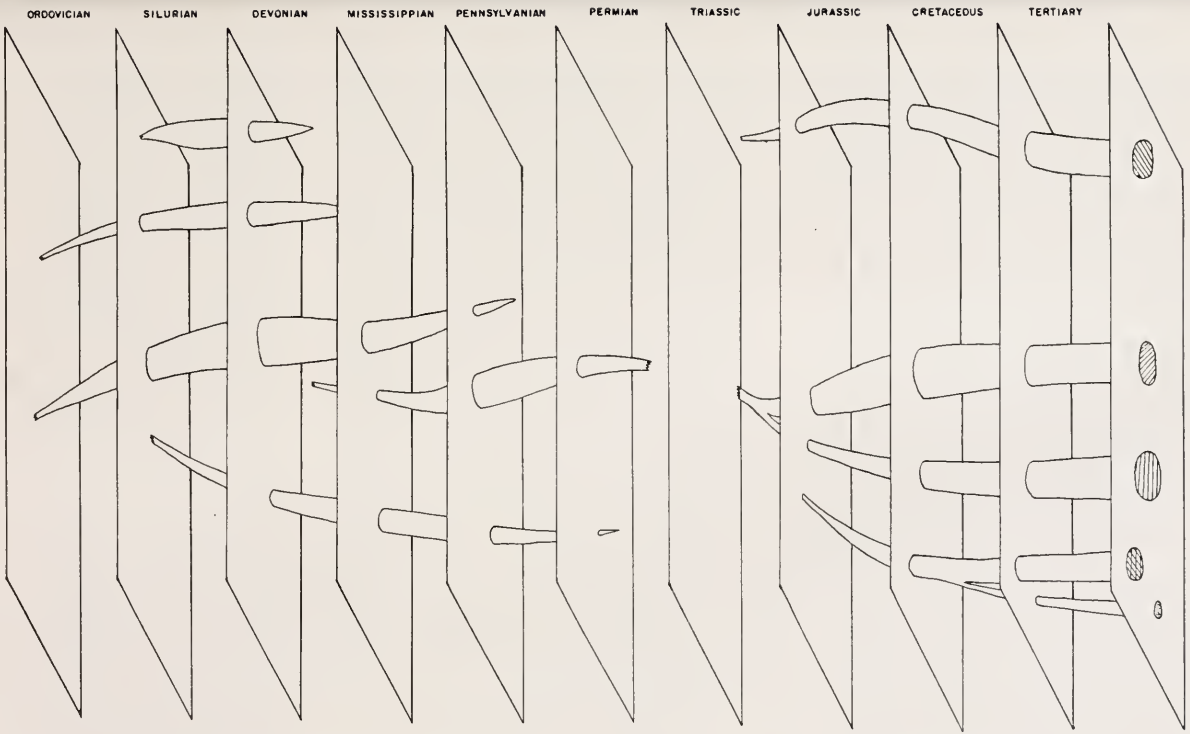

Fig. 5. Evolutionary pattern of rugosan and scleractinian suborders.

septal insertion. Further, this necessitates acceptance of a monophyletic derivation by typostrophic proterogenesis from some early ontogenetic stage of the tylolytic late Permian corals. All of this is assuredly a large order, even for typostrophism. In addition, the Scleractinia, like the Rugosa, are apparently not monophyletic (Fig. 5). At the earliest appearance of both orders, we perceive that each already contains widely divergent groups on the subordinal level, such as the columnariids in the Rugosa, and the astrocoeniids in the Scleractinia. Survival of aspects of the rugosan mode of septal insertion in scleractinians (Schindewolf, 1942; whence Cloud, 1948, and Moore *et al.,* 1952), indicative of transitional characters, seems to be more apparent than real, even more curious modifications in scleractinian septal insertion being overlooked. The question is not likely to be settled for some time.

In recent years the ceaseless search for petroleum has resulted in the discovery of more and more ancient reef structures, especially in the Paleozoic rocks. This has focused attention on the natural history of bioherms and biostromes as organic associations. Some indication of the extent of work on ancient and modern reefs is given by a recent bibliography (Pugh, 1950) which, although incomplete, still lists some 1200 titles. While relatively few of these contribute much to real ecological understanding of reefs, from them emerges the realization that Paleozoic rugose corals were not important as reef constructors, and that the real reefs of the Paleozoic were largely the work of algal and algoid organisms (mostly of uncertain affinities), aided to some extent by tabulate and stromatoporoid corals. Further, few of these structures had the wave-resistant qualities of modern oceanic reefs, possibly because few, if any, of the known Paleozoic reefs were oceanic.

This understanding results from closer paleoecological and sedimentological studies of Paleozoic reefs and from the extensive ecological work done on Recent corals during the past 25 years (Yonge, 1940). Earlier analyses (Vaughan, 1911, *int. al.*) of ancient reef associations drew conclusions that were somewhat too broad. This does not mean that ecological principles developed from the study of living corals are not applicable to Paleozoic forms. Indeed, such studies show rather clearly why some

Paleozoic corals were significant on reefs and why others were not. Simple comparison of the growth-forms of rugose and scleractinian corals suggests that the rugose corals were unfitted for the turbulent environment of reef structures in the cumatic zone. They lacked adhesiveness, and the rootlets developed in some forms were only poor makeshifts, whereas the tabulates and stromatoporoids, found in genuine reef communities, gained stability from their encrusting or strongly adherent habit, just as all important Recent hermatypic corals are stoutly adherent basally to their substrates. Further comparison shows definite superiority in colony-formation and compactness in modern hermatypic corals, as well as in the extinct stromatoporoids and

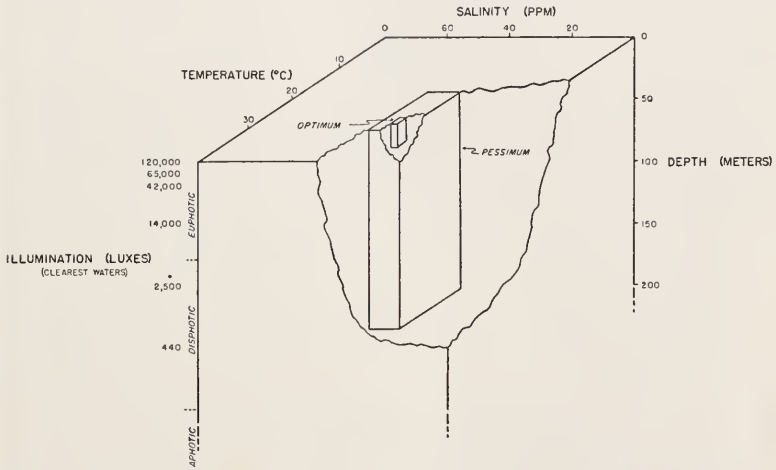

Fig. 6. Some ecological restrictions of the hermatypic corals.

tabulates. A few rugose corals were colonial, but their colonies never amounted to much. This requires some explanation beyond the limited range of modes of colony-formation available to rugosans by extratentacular budding, and their failure to develop edge-zone. Much of the answer is found in the ecological differences between living reef (hermatypic) and non-reef (ahermatypic) corals. Modern reef corals owe most of their success on reefs to an acquired symbiosis (Yonge, 1931), probably developed during the Mesozoic, with unicellular algae (zooxanthellae), a

	Recent Ahermatypic	*Rugosa*	*Recent Hermatypic*	*Tabulata*	*Stromato-poroidea*
Colonies	Solitary; few colonies	Solitary; few colonies	Large colonies	Medium colonies	Medium colonies
Corallites	separated	separated	close	close	close
Stability	variable	low	high	high	high
Reefs	rare	rare	common	common	common
Growth-rate	low	low to medium	medium to high	low to medium	low to medium?
Algal Symbionts	absent	absent	present	present?	present?
Water Temperature	temperate to cold	temperate to warm	warm	temperate to warm	temperate to warm
Light	heliophobic	heliophobic	heliophilic	heliophilic?	heliophilic?
Variety on a site	small to medium	small	large	small	small

Fig. 7. Some factors in the ecology of the principal coral groups.

curious relationship which has conferred on the corals advantages of increased metabolism or faster growth, with the concomitant potential for immensely larger colonies or populations within a given area — this to forms already structurally better fitted to the reef environment, with, however, restriction to the better-illuminated sites in warmer sea climates (Fig. 6). Recent non-reef corals lack zooxanthellae, their colonies are small, they are widespread even in temperate to cold sea climates, and are restricted mainly by sediment controls. The rugosans are analogous to the ahermatypic corals to a considerable degree.

Comparisons of some ecologic factors are suggested by the chart (Fig. 7), partly speculative and indicative of areas for further application of ecological principles. It may be suggested that the concept of warm, shallow, clear, well-illuminated tropical seas as the environment of Paleozoic corals in general, by closer analogy with the ecology of Recent corals, applies largely to the stromatoporoids and tabulates, and that the major requirements of the rugose corals were satisfied by temperate to warm (8°-18°C.) waters and not-too-rapid accumulation of sediments. But there is still much to be learned about the "ecological structure" of corals, living and fossil.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
IV. *Echinodermata: Pelmatozoa*

By Raymond C. Moore
University of Kansas, Lawrence, Kansas

INTRODUCTION

The purpose of this paper is to assess the present status of knowledge concerning fossil pelmatozoans, taking into account various important contributions which have been published during the past half century. In 1900 Bather organized his own and others' studies on all main groups of echinoderms in a well-illustrated volume of Lankester's "Treatise on Zoology"; this furnishes a very convenient starting point. Bather's lucid descriptions of morphological characters and concise outline of classification as then conceived have served during subsequent decades as an indispensable reference and, although a revision which might incorporate work done since 1900 never was prepared, the book has been reprinted again and again. Appropriately titled sections of the present paper contain brief statements of what seem to be the significant features in Bather's discussion and furnish records of various contributions which have appeared in later years.

In 1900, as generally now, echinoderms were divided into the two main groups called Pelmatozoa (more or less permanently fixed during life) and Eleutherozoa (free-moving); it is unimportant that Bather designated these assemblages as "grades," rather than subphyla or superclasses. The Pelmatozoa were distributed in four classes, respectively named Edrioasteroidea, Cystidea, Blastoidea, and Crinoidea. Jaekel's (1899) proposal to remove from among cystoids the peculiarly flattened forms which he named Carpoidea was not considered by Bather until after 1900 but the group was accepted by Schuchert (1904) and others as an independent class and now generally is so treated (although the name Heterostelea Jaekel, 1899, is used by some). Other classes called Eocrinoidea (Jaekel, 1913) and Paracri-

noidea (Regnéll, 1945) have been introduced also. The relegation of blastoids to rank as a subclass of the cystoids, as recently proposed by Regnéll (1945), is a backward step which is not accepted.

CARPOIDEA

The carpoids, which include ovoid to unevenly angular primitive echinoderms having a dorso-ventrally much flattened theca composed of few to many plates and generally a very peculiar

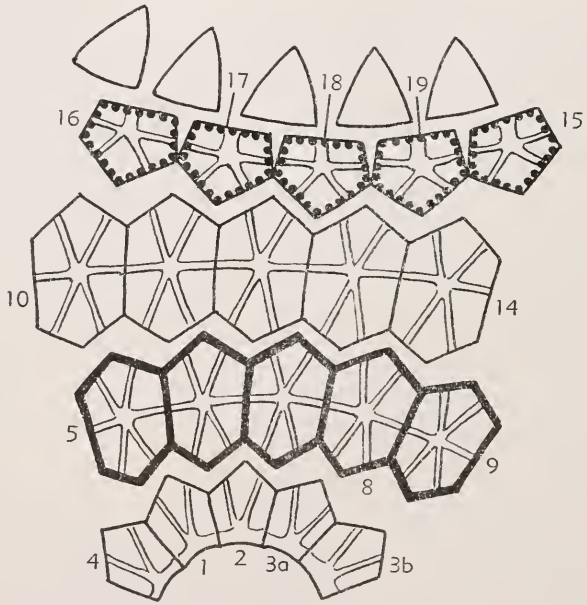

Fig. 1. Analysis of thecal structure of regular eocrinoids and rhombiferan cystoids. In upward order, the alternately disposed circlets commonly are designated as basals, infralaterals (outlined by heavy black lines), laterals, radials (outlined by heavy black dots), and orals. Numbers for identification of individual plates are indicated according to the system of Forbes (1848), based on Rhombifera. The exterior of plates other than the orals typically (or primitively) bears a pattern of ridges which is confluent across midpoints of suture lines with the markings on adjacent plates, and among rhombiferan cystoids the pore rhombs are similarly arranged.

tail-like stem appendage that narrows to a point, are chiefly Cambrian and Ordovician fossils but some specimens assigned to this group occur in rocks as young as Devonian. Typical genera include *Trochocystites*, *Mitrocystites*, *Anomalocystites*, *Placocystites*, *Cothurnocystis*, *Lagynocystis*, *Ceratocystis*, and *Dendrocystites*. All of these forms known to Bather in 1900 were assigned to two families of an order of cystoids called Amphoridea, a heterogeneous assemblage which no longer is recognized. The Carpoidea contain such strange, peculiarly modified echinoderms of several sorts that interpretation of them as representatives of a lineage standing widely separated from other groups is inescapable. Important additions to knowledge of them have been made by Bather (1913), Chauvel (1939-41) and Hecker (1940), but in general they remain poorly known and not at all adequately understood. Gislén (1927) has published on some carpoids but also has undescribed specimens.

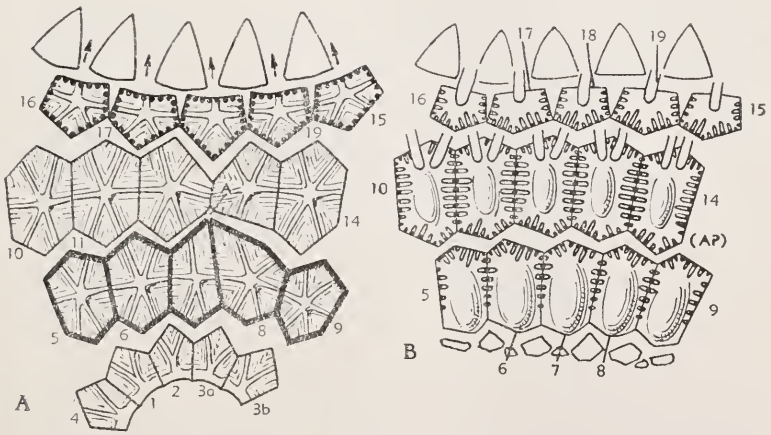

Fig. 2. Plate arrangement of regular eocrinoids. *A*, *Macrocystella*, Tremadocian (?U.Cam.), England; position of anus indicated by "A"; arrows denote brachioles attached to radials. *B*, *Lichenoides*, Middle Cambrian, Czechoslovakia, showing proximal parts of brachioles on both radials and laterals and epispires along sutures; basals are very small, irregular, and their exact number unknown; position of anus not determined. (After Ubaghs.)

EOCRINOIDEA

The Class Eocrinoidea (Jaekel, 1918) was distinguished on the basis of noncystidean features of the theca associated with the occurrence of biserial brachioles such as characterize the cystoids. A typical example is *Cryptocrinus*, which has an ovoid theca composed of three circlets of plates below the small tegmen where five pairs of brachiole facets are found. Because neither pore rhombs nor diplopores penetrate the plates, this echinoderm was placed by Bather in an order called Aporita and classed with the cystoids. Detailed studies of *Cryptocrinus* by Yakovlev (1917-27) led him to conclude that it was derived from rhombiferan cystoids but assignable to a primitive group of crinoids. Regnéll (1945) refers *Macrocystella* and other genera of the Macrocystellidae to the Eocrinoidea, whereas Bather thought that, despite lack of pore rhombs, they belonged in the order Rhombifera of the cystoids. The plates are imperforate but their outer surface bears ridges and grooves disposed approximately normal to suture lines between the plates and so spaced that the surface markings are confluent from one plate to another (Figs. 1, 2*A*). Another genus, *Lichenoides*, which was included in the Macrocystellidae by Bather but now separated in a family of its own, is a remarkable eocrinoid that recently has been studied carefully and described by Ubaghs (1953). Unlike other known early pelmatozoans, *Lichenoides* is demonstrated to have possessed two circlets of brachiole-bearing plates near the summit of the theca (Fig. 2*B*). The restoration of this fossil by Jaekel (1918), copied in various textbooks, is erroneous in showing only a single circlet of such plates with five brachioles all together, and there are other important inaccuracies. Margins of the thecal plates carry surficial canals that lead to pores located along the suture lines; they constitute so-called epispires (Hudson, 1915) which superficially resemble cystoidean pore rhombs but differ in the lack of internal canals or sacs. It is noteworthy that primitive crinoids such as *Palaeocrinus* and *Carabocrinus* among inadunates and *Cleiocrinus* among camerates have seemingly identical structures. The eocrinoids have a known range from Lower Cambrian to Middle Ordovician.

PARACRINOIDEA

Regnéll (1945) introduced the Paracrinoidea as a class of pelmatozoans which is defined by lack of polymeric symmetry of their generally numerous thecal plates, absence of distinction between dorsal and ventral parts of the theca, and the occurrence of uniserial armlike appendages. Typical genera are *Comarocystites*, considered by Bather as a representative of the cystoids (Rhombifera), and *Canadocystis;* a number of other forms are doubtfully included in the group. Clearly, these fossils, all of Middle Ordovician age in so far as known, differ markedly from crinoids and they seem to be distinct from true cystoids. The pore-rhomb structures that characterize all thecal plates of *Comarocystites* are highly developed but unusual.

EDRIOASTEROIDEA

The edrioasteroids are distinctive, somewhat aberrant pelmatozoans, characterized by the many-plated flexible nature of their upper surface which bears the mouth, anus, and generally curved ambulacra. They first appear in Cambrian rocks and persist into the Carboniferous. Most of them are discoid, but a few, such as *Pyrgocystis,* have a stalklike cylindrical form. One genus, *Astrocystites,* rather strikingly simulates a blastoid in appearance. First described by Billings in 1854, a dozen genera had become known by 1900 and since that time some 15 additional ones have been defined. They are currently divided among seven families. Chief publications on the edrioasteroids since 1900 are a series of papers by Bather (1915), Bassler (1935-36), and Cuenot (1948).

CYSTOIDEA

The early Paleozoic pelmatozoans called cystoids were understood in 1900 to embrace a wide variety of supposedly most primitive thecate echinoderms. A majority of them are characterized by very large numbers of irregularly arranged plates and associated lack of well-defined symmetry. Also, the plates commonly are perforated by rounded pores or indented by slits that open on the interior of the theca or communicate with thin-walled saclike canals. Slender armlike appendages, which are almost

exclusively biserial in structure and unbranched, may arise from the tegminal area, or subvective systems leading to the mouth may extend across the surface of thecal plates. Bather divided this assemblage into orders called Amphoridea, Aporita, Diploporita, and Rhombifera and he arranged among them genera which now are removed to the classes called Carpoidea, Eocrinoidea, and Paracrinoidea. Many forms that remain classified as cystoids exhibit constancy of plate arrangement but not well-developed radial symmetry. A few are both regular and symmetrical and among these some offer problems in classificatory assignment.

Now known genera of cystoids are approximately 90 in number, of which some 40 belong to the order Diploporita, characterized by abundance of relatively small plates pierced by almost universally paired pores, and the remainder are assigned to the order Rhombifera. The latter mostly have larger and far fewer plates, which in many genera exhibit a regularity of arrangement that permits application of a scheme of individual plate designations, and determination of homologous thecal elements. Instead of pores, the rhombiferan cystoids possess slitlike openings or internal parallel canaliculate structures that cross sutures between the plates approximately at right angles; in simplest form, the groups of slits or canals occupy rhomb-shaped areas located half on one plate and half on an adjoining plate but the external appearance of specialized pore rhombs (as in pectinirhombs) is considerably modified. An evident trend in evolution is toward reduction in the total number of pore rhombs and their localization on particular parts of the theca. Advance in knowledge of kinds of cystoids, during the last half century, is indicated by tabulation of genera recorded in 1900 (25 diploporites and 32 rhombiferans) as compared with present-day numbers (approximately 40 and 50, respectively). The most important published studies since 1900 are papers by Bather (1913) on Middle and Upper Ordovician cystoids of the Girvan district, southern Scotland; Jaekel (1918) on general structure and taxonomy; Chauvel (1939-41) on Ordovician forms from France; Hecker (1940) on fossils from northwestern Russia; and Regnéll (1945-51) on Ordovician and Silurian cystoids from Sweden and Belgium.

Diploporita. Some of the diploporite cystoids display noteworthy resemblance to other groups of echinoderms, for example,

the five spirally curved subvective pathways on the summit of *Gomphocystis,* which is strikingly like the pattern on the upper surface of various edrioasteroids; also *Proteroblastus* and *Asteroblastus* which rather closely simulate blastoids. Bather actually classified *Asteroblastus* as a primitive sort of blastoid, in spite of the presence of diplopores and occurrence of an indefinite number of irregularly arranged plates. The recently published Traité de Paléontologie (tome 3, 1953) conveniently but ambiguously places this genus and the family Asteroblastidae both in the chapter on cystoids and in that on blastoids. Actually, the diploporite group of cystoids seems to comprise an assemblage that disappeared without issue. Their known range is from lower Middle Ordovician to Devonian.

Rhombifera. The rhombiferan cystoids merit special notice because many of them have features closely similar to regular eocrinoids, suggesting genetic relationship to various groups of crinoids, on one hand, and to blastoids, on the other. Although homologies of several sorts have been noted by several workers between pore-rhomb structures and the hydrospires of blastoids, neither Bather nor anyone else seems seriously to have explored the possibilities that beginnings of evolutionary differentiation leading to typical eublastoids and to such diverse crinoids as dicyclic inadunates like *Palaeocrinus* and *Porocrinus,* and all kinds of dicyclic and monocyclic camerates, may exist within this type of cystoids or the eocrinoids. One purpose of this paper is to point out what seems to be previously overlooked ways in which several puzzling characters of plate arrangements which are diagnostic features of these noncystoid pelmatozoans may be explained. Accordingly, the organization of several representative rhombiferan genera will be illustrated and discussed briefly.

Rhombiferans of the family Echinosphaeritidae are judged to be the most archaic representatives of the order both because they are among the oldest known and because they have the most numerous thecal plates, virtually all of which are occupied completely by an unspecialized type of pore rhombs. The exterior of unusually well-preserved specimens may be nearly smooth, as in *Echinosphaerites,* or very strongly marked ridges running transverse to plate sutures may form a distinctive pattern over all of the theca, as in *Caryocystites, Orocystites,* and *Heliocrinites.*

Forms like some of these genera may very well correspond to ancestors of the Cheirocrinidae and other families having more stable structures, which also are more specialized, but because

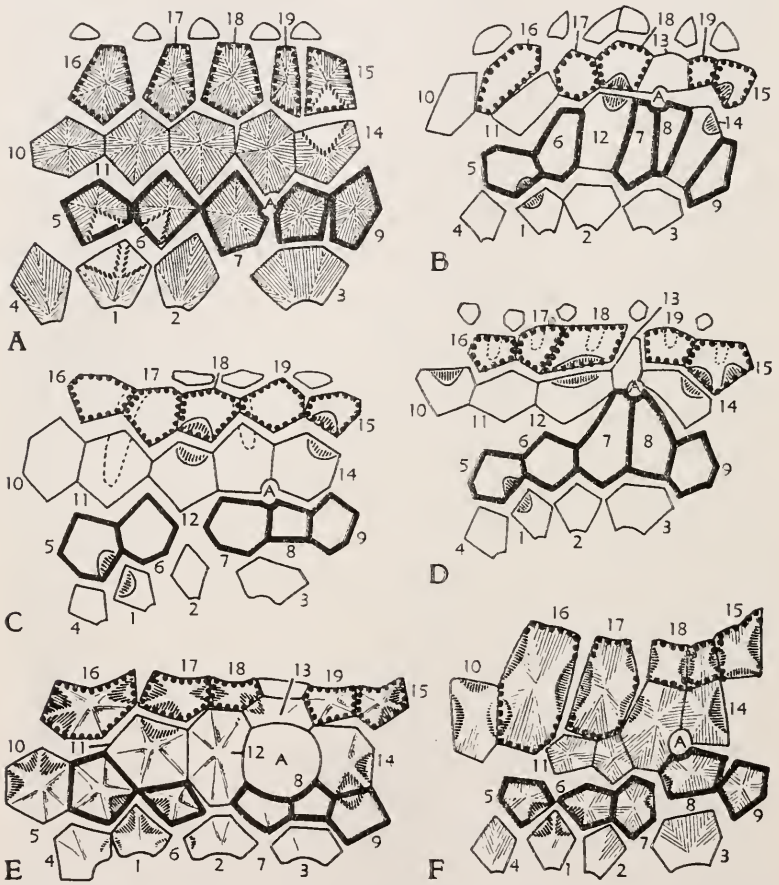

Fig. 3. Plate arrangement of rhombiferan cystoids (laterals and radials differentiated as in Figure 1 and position of anus marked by "A"). The diagrams illustrate stability in placement of pore rhombs on plates 1 + 5, 12 + 18, and 14 + 15 and they demonstrate tendency of various plates to change in shape and position. *A, Echinoencrinites,* M.Ord.; *B, Callocystites,* M.Sil.; *C, Schizocystis,* M.Sil.; *D, Lepadocystis,* U.Ord.; *E, Cheirocrinus,* M.Ord.; *F, Glyptocystites,* M.Ord. (All modified from Bather.)

homologous elements of these latter are better recognizable, attention will be confined to them.

The most regular, simply constructed sort of cheirocrinid has a theca composed of four 5-plate circlets disposed in alternating position beneath a tegmen formed of five small plates corresponding to orals. The arrangement of these elements and the system of numbers for designation of them introduced by Forbes (1848) are illustrated in Figures 3 and 4. Pore rhombs of unspecialized sort occur on a majority of the plates in the most primitive genera, as for example in *Glyptocystites* (Fig. 3*F*), but they are progressively reduced in number and increasingly modified in type as seen in genera which must be interpreted as advanced.

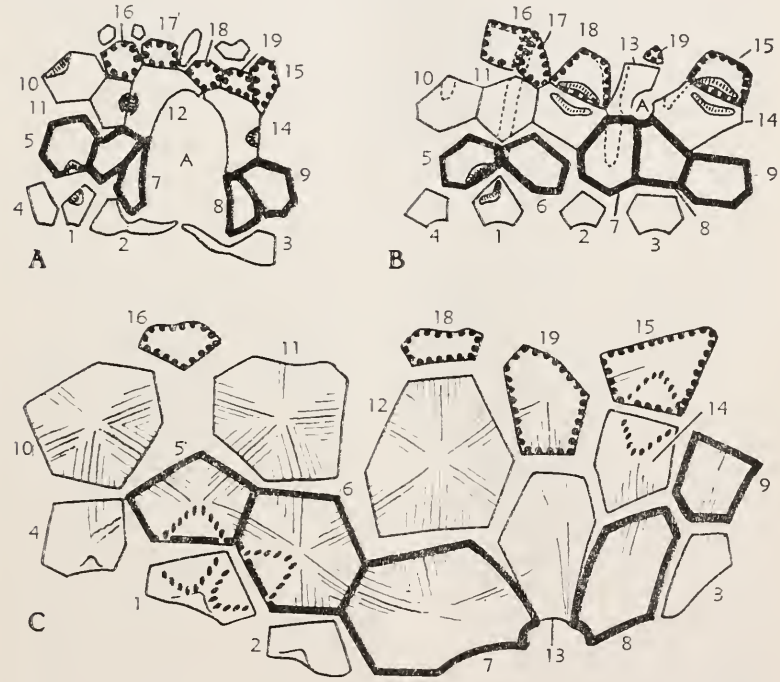

Fig. 4. Plate arrangement of rhombiferan cystoids (laterals and radials differentiated as in Figure 1 and position of anus marked by "A"). *A*, *Pleurocystites*, M.Ord.; *B*, *Lovénicystis*, U.Sil.; *C*, *Proctocystis*, M.Ord. (Modified from Bather, *A*, and Regnéll, *B*, *C*.)

The most persistent pore rhombs are those located on plates 1 + 5, 12 + 18, and 14 + 15. In several genera of this group, such as *Echinoencrinites*, *Glyptocystites*, *Cheirocrinus*, *Pleurocystites*, and *Proetocystis*, thecal plates are marked externally by parallel ridges and grooves that meet suture lines transversely in such a manner as to be confluent with similar markings on neighboring plates. Their pattern exactly corresponds to that of simple pore rhombs in forms like *Echinosphaerites* and they closely resemble the plates of the eocrinoid *Macrocystella*, also. It is altogether reasonable to interpret them as traces or derivatives of once-functional pore rhombs. They may dwindle into marginal corrugations and along suture lines be represented by regularly spaced pits that hold bundles of ligamentous fibers. They may disappear entirely. These observations of plate features in rhombiferan cystoids, and likewise in eocrinoids, probably have significance in understanding the more or less identical characters of many crinoid plates.

Another important generalization derivable from comparative study of these cystoids relates to placement of the food-gathering subvective structures. In several genera they lie recumbent on the thecal plates radiating from the tegminal region, becoming rather closely similar to blastoids in such forms as *Lepocrinites*, *Proteroblastus*, and *Cystoblastus*. The brachioles also may be free appendages rising from the summit part of the theca.

In spite of stability expressed by the almost invariable enlargement of plate 3 in the lowermost circlet and constancy in placement of pore rhombs, various genera show noteworthy downward and upward shifts in position of some thecal plates along with change in the plate outlines. In this way, the complement of plates in a given circlet may be enlarged or reduced and the latter sort of change may be effected also by complete disappearance of thecal plates. Thus, modifications in the architectural pattern of the whole theca are introduced. It is interesting to learn that the position of the anal opening is almost invariably above or between plates 7 and 8 of the next-to-lowermost (infralateral) circlet.

Before leaving the cystoids, it is desirable to notice forms which are grouped in the family Caryocrinitidae, for these have mostly very regularly arranged plates in three circlets below the tegmen

and they exhibit distinct trimerous (or hexamerous) symmetry. *Hemicosmites* and *Caryocrinites* are examples (Fig. 5). Pore-rhomb canals, which are well developed on the inner side of plates, do not appear externally, although their presence is

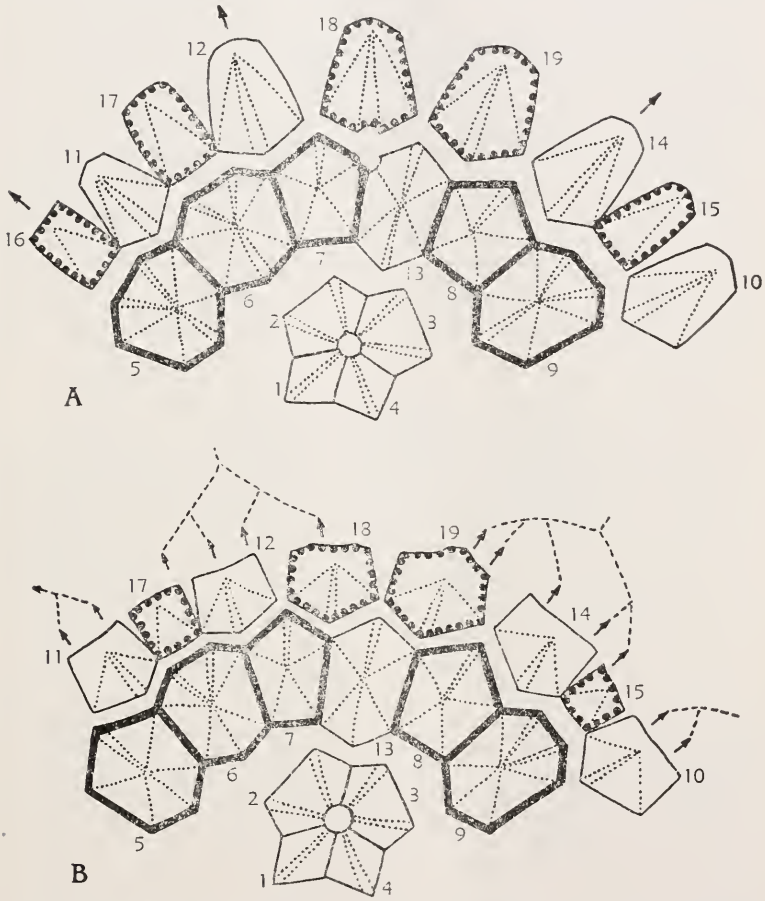

Fig. 5. Plate arrangement of hexamerally symmetrical rhombiferan cystoids showing inferred correlation with elements of other regular rhombiferans (as illustrated in Figs. 3 and 4); arrows mark location of brachiole facets. *A, Hemicosmites,* M.Ord.; *B, Caryocrinites,* M.Ord.-M.Sil. (Modified from Bather.)

marked by rows of tubercles running from the center to angles of the plates; these tubercles comprise the thin covering of slightly produced pores at borders of the rhombs. Bather applied nomenclature of dicyclic crinoids to these cystoids, designating the lowermost circlet as infrabasals, the intermediate one as basals, and that next to the tegmen as radials and interradials (although neither distribution of brachioles, or arms, nor disposition of plates in this third circlet furnish basis for distinction of radials from interradials). The whole pattern of thecal structure is explainable readily by downward migration of one plate from the circlet of "laterals" (probably no. 13) in the 4-circlet regular Rhombifera and upward migration of the others. A feature that suggests affinity with camerate crinoids (as noted by Bather) is the subtegminal placement of the proximal part of food passageways leading to the mouth. *Caryocrinites* possesses typical pinnulate biserial arms of camerate type (Springer, 1926, pl. 33, fig. 37).

BLASTOIDEA

The Class Blastoidea is generally distinguished from cystoids by the very regular pentameral symmetry of the budlike theca composed of plates which ordinarily are reckoned to be reduced in number to 13 (three basals, five radials, and five interradially disposed deltoids). Actually five lancet plates occur also, placed along the midline of each radial, but they are concealed by numerous small side plates of the recumbent ambulacra. Abundant threadlike brachioles are joined to edges of the ambulacra. Bather divided the group into "grades" called Protoblastoidea and Eublastoidea, the former including *Blastoidocrinus, Asteroblastus*, and *Asterocystis*, whereas the latter comprises all others. Although Bassler (1938), and Bassler and Moodey (1943) have followed this classification, adding *Mesocystis* to the Protoblastoidea, most students assign all of these named genera, except *Blastoidocrinus*, to the cystoids and generally they do not recognize a division (order) called Protoblastoidea. Probably the most noteworthy contributions to the knowledge of blastoids during the last half century are the studies of Hudson (1907), who defined the order Parablastoidea; Jaekel (1918), who recognized the importance of hydrospire openings in classifying the Eublast-

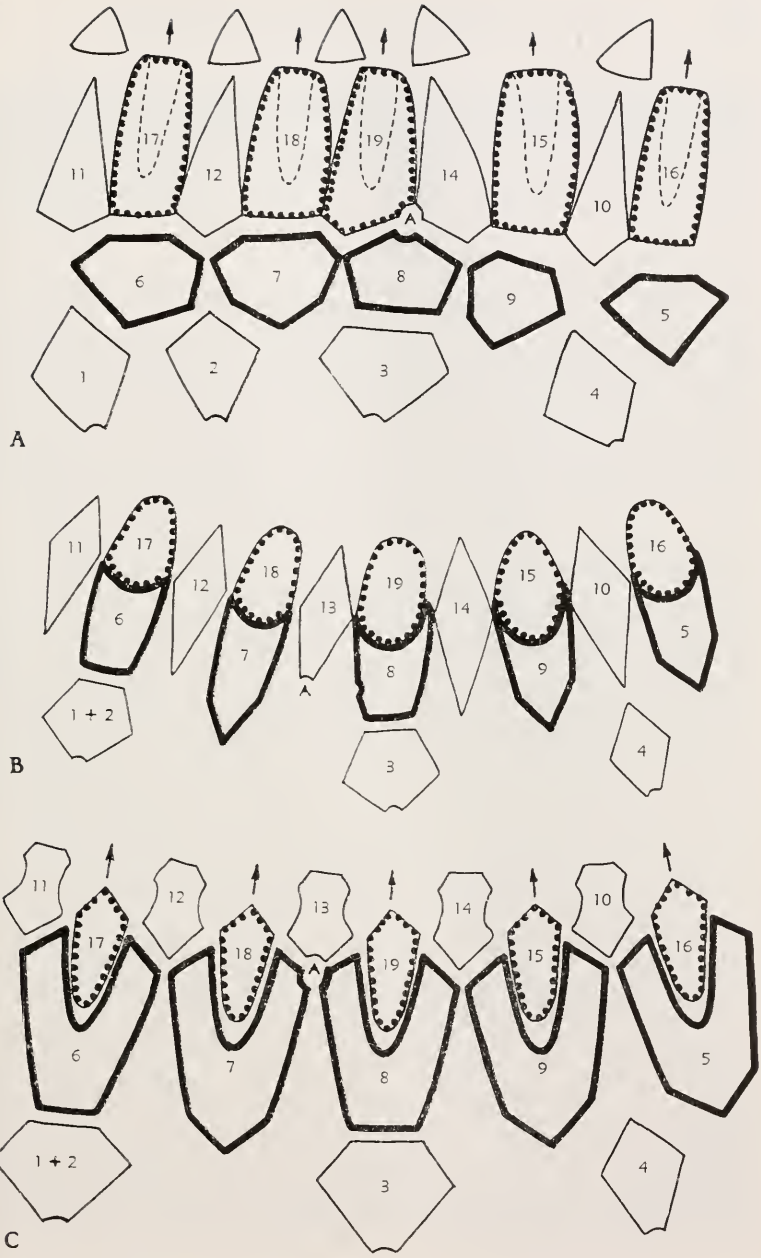

Fig. 6. *A*, plate arrangement of a regular rhombiferan cystoid, *Cystoblastus*, M.Ord. *B*, hypothetical evolutionary derivative of a pre-*Cystoblastus* type and *C*, a typical eublastoid in which correlation with elements of presumed rhombiferan ancestral stock is indicated by differentiation of circlets as in Figure 1. Arrows denote position of ambulacra and "A" location of the anus. The blastoid radials are identified as rhombiferan infralaterals, lancet plates as rhombiferan radials, and deltoids as rhombiferan laterals.

oidea by introducing suborders called Fissiculata and Spiraculata; Wanner (1924-49), who described many remarkable blastoids from Permian rocks of Timor; Cline (1936-44), who specially studied some Mississippian genera; and Bergounioux (1953), who surveyed morphology and taxonomy of the class. On the whole, however, advance in this period is considerably smaller than one might expect.

An absorbing problem on which no real progress has been made for a very long time relates to the origin of the blastoids. That the group has strong cystidean affinities is very evident — so much so, indeed, that Regnéll (1945) ill-advisedly proposed to rank the Blastoidea as a subclass of the cystoids. Yet no one thinks that evolution leading to the eublastoids can be traced from such blastoid-like cystoids as *Proteroblastus*, *Asteroblastus*, or *Cystoblastus*. What then are the roots of blastoids? Observation of the structure and evolutionary trends shown by the regular rhombiferan cystoids leads me to suggest a previously unexplored line of attack. Remembering that thecal elements of the 4-circlet cheirocrinids show tendencies to shift positions and shapes, as clearly illustrated by *Cystoblastus* (Fig. 6*A*), is it conceivable that the ultimately very stable features of eublastoid structure may be derived from this source? A postulate in this direction is offered diagrammatically by Figures 6*B* and 6*C*, in which a hypothetical intermediate cystoid-blastoid, descended from a somewhat *Cystoblastus*-like ancestor, is succeeded by a form having all of the structural characters typical of the true blastoids. If this concept accords with the actual course of evolutionary change, it becomes evident that such elements as the lancet plates are fundamental parts of blastoid anatomy, being derived from the uppermost circlet (so-called radials, nos. 15-19) of the regular rhombiferans, whereas the deltoids are upwardly moved laterals (nos. 10-14) in interradial position. Fusion of two pairs of lowermost-circlet plates of the presumed rhombiferan ancestor yields the characteristic basal circlet pattern of the eublastoids, with the small (azygous) basal in the antero-right position. The hydrospires, as perhaps most simply shown in *Codaster*, are strictly homologous to the pore rhombs in the Rhombifera, transecting the sutures between radials and deltoids approximately at right angles, and study of them in thin sections

under polarized light demonstrates crystallographic continuity of different parts of each hydrospire with thecal plates which they adjoin. Thus, derivation of the blastoids from rhombiferan cystoids of seemingly very unlike thecal organization becomes a rational hypothesis.

CRINOIDEA

By far the largest and most varied division of the Pelmatozoa consists of the crinoids. Without doubt, also, this class contains the most highly evolved members of the subphylum, as well as the only representatives found in post-Paleozoic deposits. More than 5,000 species of fossil crinoids have been described, which is several times the number of all other pelmatozoans combined. Naturally, therefore, the Crinoidea have preeminent importance in paleontological study of fixed echinoderms.

Crinoids are distinguished by almost universal well-developed symmetry of the theca (calyx), and presence almost without exception of relatively strong, prominent arms which may be many-branched and very commonly provided also with innumerable branchlets (pinnules). A more or less elongate stem composed of generally discoid, centrally pierced plates (columnals) serves as a means of attachment, although many crinoids (especially modern comatulids) are stemless in adult life. Stratigraphic range of the class is from Tremadocian (?Upper Cambrian) to Recent.

In 1900, all main kinds of crinoids were fairly well known but the classification accepted by Bather and generally adopted by other workers of the time is radically different from that prevailing now. Of course, much new information has been gained from study of innumerable genera which then were unknown and the interpretation of various morphological features has changed. Crinoid genera known in 1900 numbered about 250, whereas additional genera described since 1900 are about 500. Bather divided all crinoids into subclasses called Monocyclica (having only a single circlet of plates below the radials) and Dicyclica (having two circlets below the radials). The monocyclic group contained orders named Inadunata, Camerata, and Adunata, whereas the dicyclic group contained orders named Inadunata, Camerata, and Flexibilia, thus duplicating some of the ordinal

designations. Not only by this classification but by Bather's discussions the conclusion is expressed that monocyclic inadunates (like *Pisocrinus*) and monocyclic camerates (like *Actinocrinites*) are much more closely related to one another than respectively to dicyclic inadunates (like *Cyathocrinites*) and dicyclic camerates (like *Rhodocrinites*). This was denied by Springer (1913) and has come almost universally to be rejected. Wachsmuth and Springer (1885) divided the Inadunata into assemblages called Larviformia (dominantly monocyclic) and Fistulata (dominantly dicyclic) which, although widely accepted in publications as late as 1943 (Bassler and Moodey), have been displaced by differently defined orders named Disparida, Hybocrinida, and Cladida (Moore and Laudon, 1943; Jaekel, 1918; Regnéll, 1948; Ubaghs, 1953). The Camerata are divided into orders called Diplobathrida and Monobathrida (Moore and Laudon, 1943; Ubaghs, 1953). Post-Paleozoic crinoids are grouped in the Subclass Articulata.

It is impractical to review here the voluminous literature on crinoids which has appeared during the past half century and accordingly mere mention of selected contributions that seem to have most significance must suffice. These include in foremost place: (1) many long and short papers by Frank Springer (1900-26), especially his monographs on the Flexibilia and American Silurian crinoids which not only furnish organization of a vast amount of accumulated studies but importantly extend the frontiers of knowledge; (2) A. H. Clark's (1908-41) additions to understanding of the morphology and classification of articulate crinoids, especially in monographs on living forms; (3) Kirk's (1911-50) discussion of eleutherozoic crinoids and numerous short papers on various genera; (4) James Wright's (1913-53) comprehensive studies of British Carboniferous crinoids, including description of many new forms; (5) Wanner's (1916-49) invaluable enrichment of information pertaining to Permian crinoids and penetrating interpretation of their relationships; (6) Jaekel's (1918) taxonomic survey and discussion of the phylogeny of all pelmatozoans; (7) Goldring's (1923) large memoir on Devonian crinoids of New York; (8) Gislén's (1924-38) work on fossil and living articulates; (9) Sieverts-Doreck's (1927-52) numerous papers; (10) W. E. Schmidt's

(1930-42) studies of Devonian and Carboniferous crinoids of Germany; (11) work by Moore (1940-52), Moore and Laudon (1943-44), and Moore and Plummer (1937-40) describing many late Paleozoic crinoids and revising classification; (12) Teichert's (1949) report on Australian *Calceolispongia;* (13) Termier and Termier's (1949) effort to correlate structural characters of crinoid groups; and (14) Ubagh's (1943-53) thorough investigation of some European genera and able general account of crinoids representing all types. Collectively, these and the work of many not mentioned may be accounted at least to have matched the progress made in the investigation of crinoids from the time of J. S. Miller's (1821) "Natural History of the Crinoidea, or Lily-shaped Animals" down to 1900.

Origin of some crinoid stocks. The oldest known crinoid seems to be a rather poorly described inadunate (called *Dendrocrinus cambriensis* Hicks) from Tremadocian rocks of England, variously assigned to uppermost Cambrian or lowermost Ordovician. Very little later and almost coincidentally, many representatives of the Inadunata, Camerata, and some Flexibilia made their appearance. The origin and interrelationships of these crinoid groups have been studied again and again without arriving at any firm conclusions but it is agreed that in each group various stable features are distinguishable from the very beginning. For example, among flexible crinoids this applies to the peculiarities of ray structure and constant arrangement of infrabasal plates (two large and one small, the latter invariably in right posterior position except in rare aberrant individuals). In the monocyclic camerate group called Tanaocrinina, the insertion of an anal plate (tergal) in the circlet of radials and the hexagonal outline of the basal circlet, which very predominantly consists of three equal plates, are constant distinguishing features, whereas radials in contact with one another all around and a pentagonal basal circlet are similarly constant attributes of remaining monocyclic camerates (Glyptocrinina). The phylogenetic significance of these things, not to mention many others, remains almost wholly conjectural.

Bather gave detailed attention to homologies observed between various seemingly little related crinoids and to correspondence in structures of some crinoids and cystoids, but he rejected the

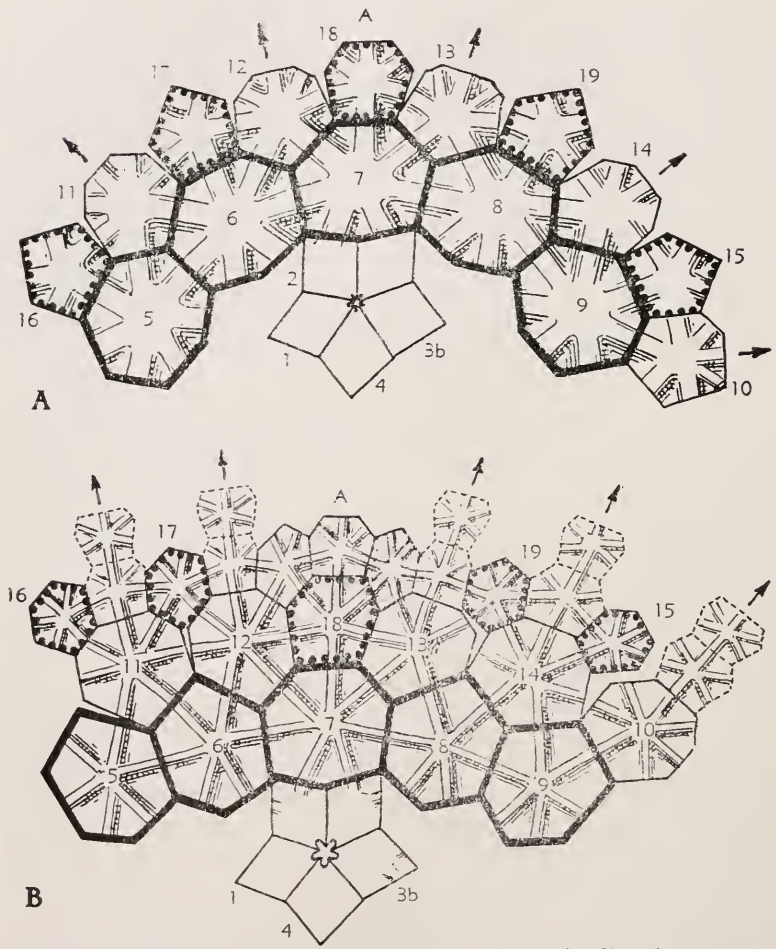

Fig. 7. Plate arrangement of lower part of cup in dicyclic camerate crinoids showing inferred correlation with thecal elements of eocrinoids and rhombiferan cystoids as differentiated in Figures 1-4. *A*, Archaeocrinidae and Rhodocrinitidae, M.Ord.-Miss.; *B*, Ptychocrinidae, Dimerocrinitidae, and Lampterocrinidae, M.Ord.-L.Dev. If derivation here suggested is correct, the brachials of each ray are developed in series with plates corresponding to laterals (as in *Lichenoides*); also, the plan of plates shown in *A* is the more advanced, which is contrary to opinion expressed by Moore and Laudon (1943).

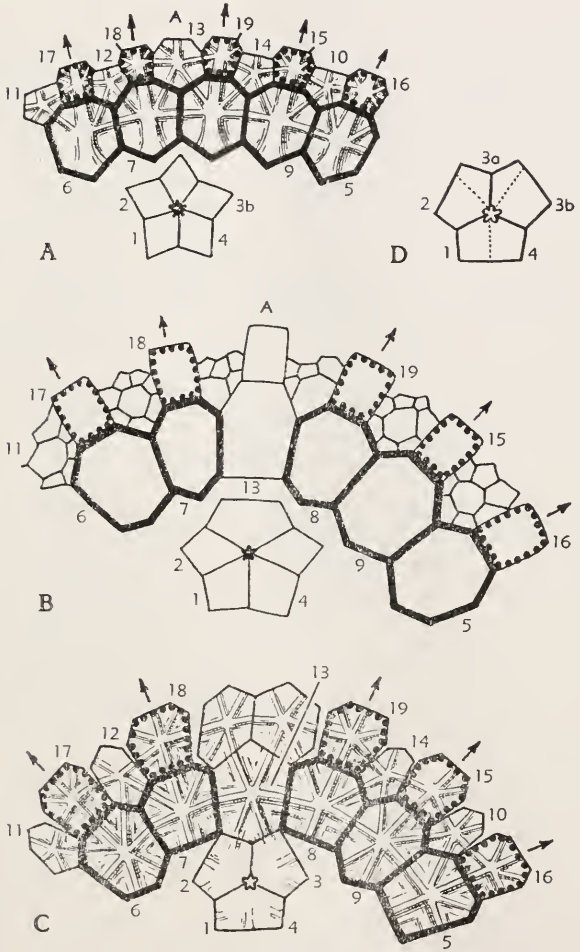

Fig. 8. Plate arrangement of lower part of cup in monocyclic camerate crinoids showing inferred correlation with thecal elements of eocrinoids and rhombiferan cystoids as differentiated in Figures 1-5. *A*, Glyptocrinina, U.Ord.-Perm.; *B*, Tanaocrinidae, U.Ord.; *C*, Actinocrinitidae, Miss.-Perm.; *D*, Plan of basal circlet in all families of Tanaocrinina except Tanaocrinidae, Dichocrinidae, and Acrocrinidae, showing orientation of pentastellate lumen and (by dotted lines) position of sutures between plates in a 5-plate circlet. If derivation here suggested is correct, the brachials of each ray are developed in series with plates corresponding to infralaterals of eocrinoids and rhombiferan cystoids; also, the ancestral stock that gave rise to the Tanaocrinina (Figs. *B-D*) must have developed the hexameral organization of caryocrinitids, whereas the Glyptocrinina descended from a normal pentameral type of eocrinoid.

postulate that rhombiferan cystoids (or pelmatozoans of this type, including forms now classed as eocrinoids) could be ancestral to any crinoid group. I undertake here to demonstrate by diagrams (Figs. 7, 8) that the respective dorsal cup patterns of all types of camerate crinoids are directly derivable from eocrinoids or conceivably from regular rhombiferan cystoids of sorts that belong either to the Cheirocrinidae or Caryocrinitidae; this calls merely for longitudinal shifting of thecal plates in a manner clearly shown within the cystoid assemblage. It is interesting to observe that, whatever the ultimate stable arrangement of cup plates in the crinoids may be, the orientation of the pentagonal or pentastellate lumen at the center of the lowermost circlet (continuous with the stem) remains constant, although where this opening is circular, orientation of the chambered organ cannot be detected. A radical innovation which is introduced by this approach to explaining camerate cup architecture is the deduction that infrabasal plates of dicyclic cups are identical to basal plates of monocyclic forms and not elements of originally different circlets. It follows that monocyclic camerates are not descendants of dicyclic camerates produced by diminution and ultimate disappearance of the lowermost circlet (so-called infrabasals). It is pertinent to call attention to the persistence of stereom folds or ridge patterns on cup plates of very many of the camerates, both dicyclic and monocyclic, reflecting the arrangement of pore rhombs belonging to their presumed eocrinoid or cystoid ancestors.

Much more lengthy discussion than can be given in this paper is needed in order to analyze the many implications of homologies which are newly suggested here. Such discussion may be undertaken in later writing. For the present, I assert only that the postulates now offered cannot plausibly be extended to embrace any of the Flexibilia nor possibly more than a very few kinds of inadunates (perhaps Hybocrinida, Carabocrinidae, Palaeocrinidae, and some others). No trace of affinities with any cystoids, eocrinoids, paracrinoids, or carpoids is recognized in the many kinds of flexible crinoids, disparid inadunates, or most of the cladids. If all camerates are descended from eocrinoid- or cystoid-like ancestors, whereas most other crinoids are not, the Class Crinoidea is polyphyletic.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
IV. *Echinodermata: Eleutherozoa*[1]

By

J. Wyatt Durham
Museum of Paleontology, University of California
Berkeley 4, California.

Inasmuch as all classes of eleutherozoan Echinodermata are well represented in the Recent faunas, a realistic appraisal of our knowledge of fossil Eleutherozoa requires a comparison with the living fauna. According to A. H. Clark (1948) there are about 1500 species of Asteroidea, the same number of Ophiuroidea, and 771 species of Echinoidea in the Recent fauna (no estimate for Holothuroidea). Mortensen (1928-1951) in his comprehensive work lists 867 species and 88 varieties of living Echinoidea. Pratt (1935) lists 1100 species of Asteroidea, 1600 species of Ophiuroidea, 600 species of Echinoidea, and 650 species of Holothuroidea as the approximate numbers of these organisms that occur in the Recent faunas. Because of his greater familiarity with the Echinodermata it seems probable that Clark's estimates are more nearly correct than those of Pratt. Clark also indicates that most of the species are inhabitants of shallow water areas, from low tide down to depths of about 1500 feet. Thus the occurrences of most living Eleutherozoa would compare favorably with the depth facies of much of the fossil record. A general survey of the literature (not exhaustive) indicates that as of 1952 there were described from the fossil record at least 300 species of Asteroidea (first record in the Ordovician), at least 179 species of Ophiuroidea (first record in the Ordovician, including about 74 species referable to the Auluroidea *auct.*), at least 3 species of Somasteroidea (restricted to Ordovician), and about 7200 species (about 4500 Irregularia) of Echinoidea (first record in the Ordovician). D. L. Frizzel (personal communication, June 19, 1953) states that he recognizes

[1] A contribution from the Museum of Paleontology of the University of California, Berkeley 4, California.

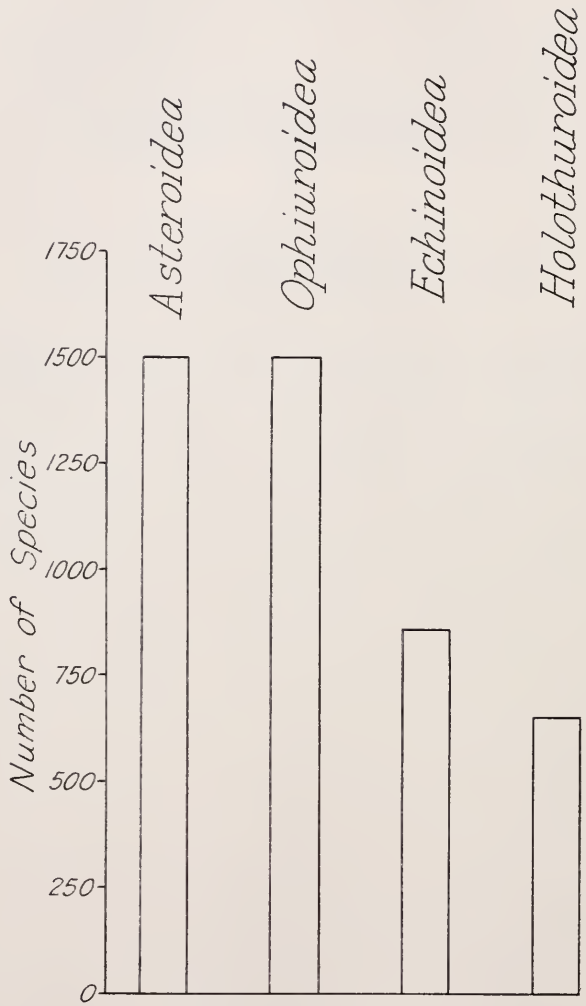


Fig. 1 Living Eleutherozoan Echinodermata Worldwide.

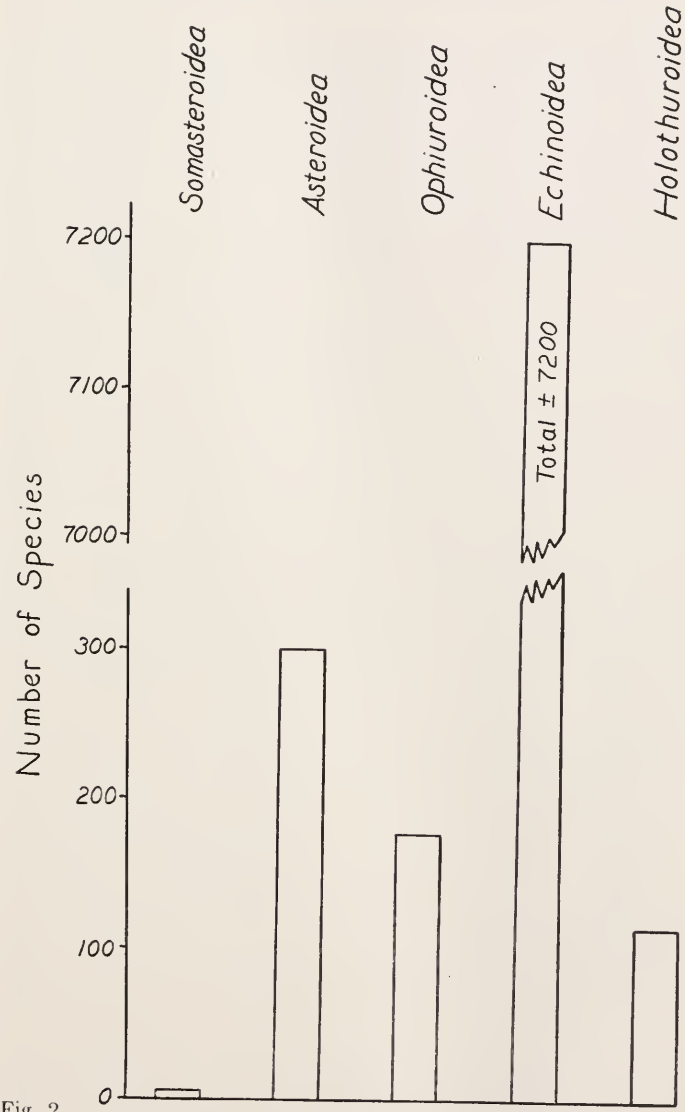

Somasteroidea
Asteroidea
Ophiuroidea
Echinoidea
Holothuroidea
Total ± 7200
7200
7100
7000
300
200
100
0
Number of Species
Reported Fossil Eleutherozoan
Echinodermata – Worldwide

Fig. 2

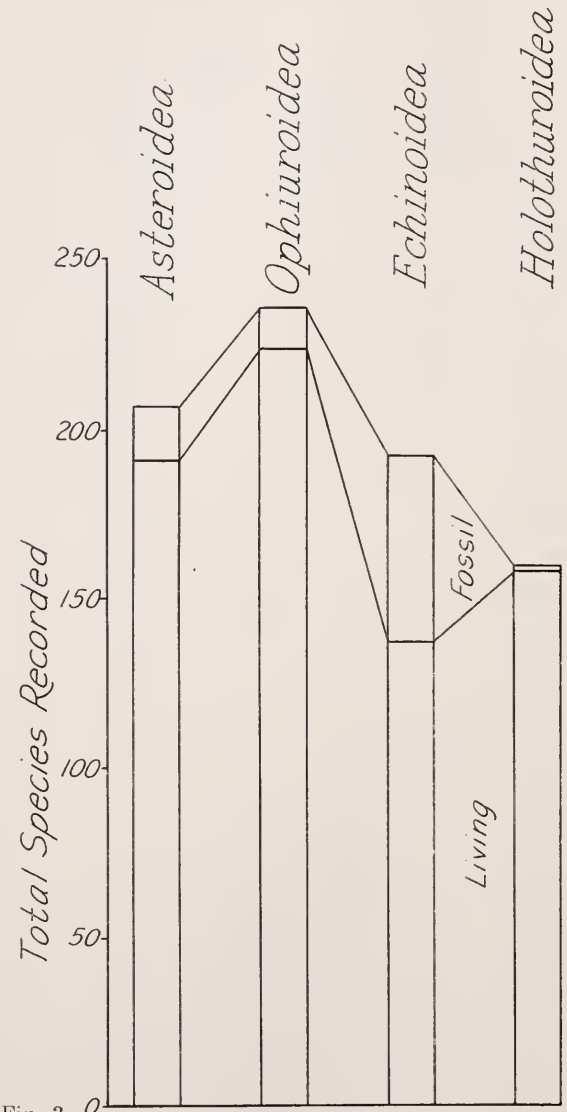


Fig. 3 Eleutherozoan Echinodermata of Australia. From Clark, 1946.

117 species of fossil Holothuroidea, beginning in the Devonian (he recognizes no pre-Devonian records as referable to the Holothuroidea). The above data are summarized in graphic form in Figures 1 and 2.

From the above data on Recent and fossil Eleutherozoa it is apparent, considering the many "turnovers" in fossil faunas that must have occurred from the early Paleozoic to Recent, that the described fossil representatives of the various classes, excepting the Echinoidea, are an extremely inadequate sample of the faunas that must have existed.

For more detailed comparisons of fossil and living faunas, data regarding occurrences within faunal provinces are illuminating. In the Australian area (Clark, 1946), there are recorded (Fig. 3) 189 living and 17 fossil asteroid species, 223 living and 14 fossil ophiuroid species, 135 living and 56 fossil echinoid species, and 158 living and one fossil holothurian species. It is obvious that in this region the fossil record is very incomplete.

On the Pacific Coast of North America (Fisher, 1911-1930; Grant and Hertlein, 1938; Clark, 1948), the present-day fauna includes about 149 species of asteroids, and about 52 species of echinoids in the region from Alaska to the Isthmus of Tehuantepec. Similar data for the Ophiuroidea and Holothuroidea is not readily available, but by analogy with the world-wide fauna and the Australian area it may be assumed that they are approximately equal in numbers to the Asteroidea and Echinoidea respectively. In the fossil record (Durham, 1950; Durham and Roberts, 1948; Eaton, Grant, and Allen, 1941; Grant and Hertlein, 1938; and other sources), about 4 species of asteroids, 10 of ophiuroids, 186 (species and subspecies) of echinoids, and no holothurians have been reported along the Pacific Coast from Alaska to the Isthmus of Tehuantepec. When these occurrences are compared (Fig. 4) with the living fauna of the same area it is readily apparent that only the echinoids are at all adequately represented in the reported fossil record.

A more detailed comparison may be made (Fig. 5) between the Recent and recorded Tertiary and Pleistocene echinoids of the Pacific Coast when the records are sorted into epochs and the scutellid echinoids segregated. Among the non-scutellid echinoids no one epoch has a recorded species representation

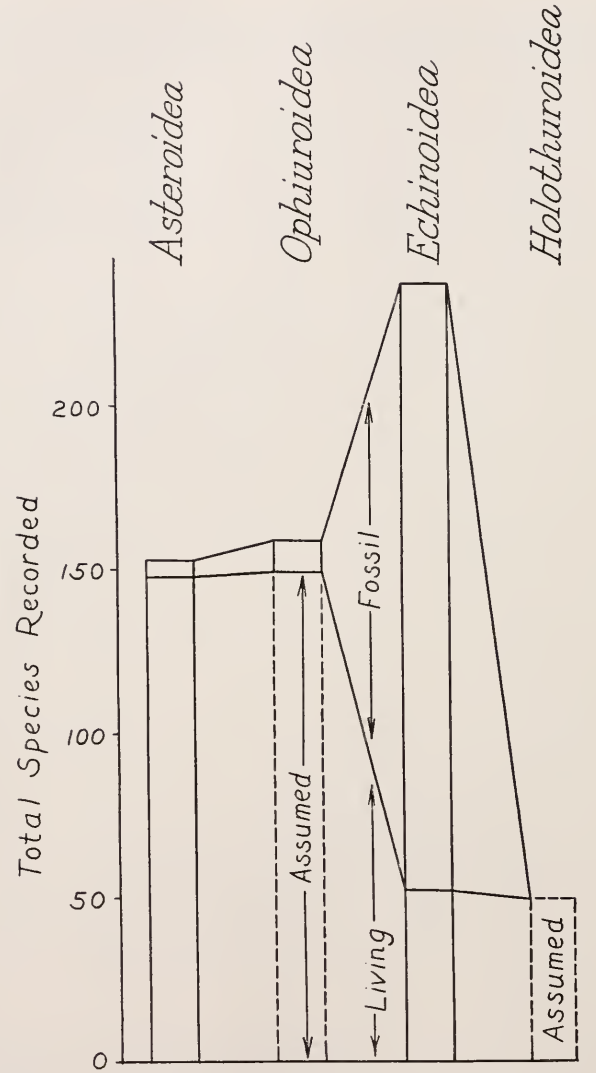
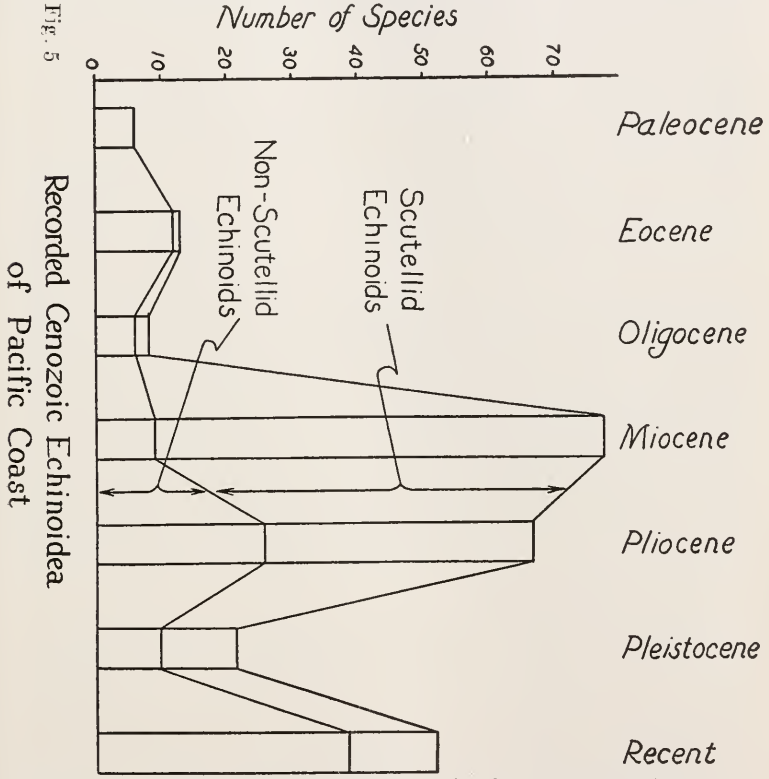


Fig. 4 Eleutherozoan Echinodermata of Pacific Coast.

equivalent to that of the Recent, but the Pliocene with 26 species approaches the Recent fauna (39 non-scutellids). The scutellid echinoids with several extinct and short-ranged genera (*Astrodapsis, Merriamaster, Scutaster,* and *Scutellaster* [=*Anorthoscutum auct.*]) as well as somewhat longer-ranging genera such as *Echinarachnius,* were obviously evolving rapidly in this area. However this apparent rapid evolution is possibly affected by a

Fig. 5



refinement of systematics not apparent in the non-scutellid group: for instance, the 37 new specific and subspecific unit names proposed in the paper by Eaton, Grant and Allen (1941) for the upper Miocene scutellids of a small area. Of the 37 names, 36 are applied within the genus *Astrodapsis* alone. Nevertheless, despite doubts that may be raised by the systematics involved, the rapid and varied diversification of the scutellids in the

Pacific Coast Neogene testifies to the evolutionary potential present in some irregular echinoid stocks under favorable conditions. Some of these scutellids are fairly widespread and common in the Neogene of the California area and serve as excellent index fossils.

Despite the apparent sparsity of their fossil record both the Asteroidea and Ophiuroidea appear to be represented in the Lower Ordovician (Spencer, 1951). Because of the excellent preservation of detail of some of the Lower Ordovician material and from theoretical considerations of the significance of some of the structures present in these early stelleroids, Spencer (*op. cit.*) has presented a new classification of this group, in part cutting across that used by Schuchert (1915). In addition to the commonly recognized subclasses Asteroidea and Ophiuroidea, Spencer proposed the new Subclass Somasteroidea for primitive starfish with the "arms" merely differentiated portions of the oral surface, with no ambulacral groove, and with a well defined oral interambulacral skeleton only in early members. Insofar as now known, the somasteroids are confined to the Lower Ordovician. The Auluroidea of Schöndorf and Schuchert as well as the Family Stenasteridae of Schuchert, which was considered to be an asteroid, are included within the Order Stenurida of the Ophiuroidea in Spencer's new classification. Spencer's orders Stenurida and Ophiurida are differentiated on the basis of whether or not the ambulacralia are modified into vertebrae (Ophiurida). On this basis the Ophiurida are also present in the Lower Ordovician.

The lack of an ambulacral groove in the somasteroids, the group including the earliest starfish known so far, causes Spencer to question the primitiveness of the groove and its significance in the search for ancestors of the group. Because of its absence, he feels that Cambrian Edrioasteroidea cannot have given rise to the starfish as has been suggested, but that some ciliary feeding echinoderm must have been their ancestor.

Among the Holothuroidea, D. L. Frizzell (personal communication, June 19, 1953) states that 9 families and 23 genera, with 117 species, can be recognized from the published records of fossil members of the group. Three species and 2 genera have been described from complete specimens from the Solenhofen

limestone. All other records are based on sclerites. All authenticated records of fossil holothurians are from Devonian or younger rocks. The supposed pre-Devonian records cannot be referred to the group.

Mortensen (1928-1951; esp. vol. 5, pt. 2, pp. 565-573) has summarized data on fossil echinoids as well as that derived from the living echinoids and presented a number of important conclusions on their phylogeny. The first of these is that *Bothriocidaris*, considered by Jackson and others to be the ancestral stock of the Echinoidea is not a true echinoid, but more probably a cystoid. The lack of an open ambulacral furrow in the Middle Ordovician *Bothriocidaris* and its occurrence in the Middle Ordovician *Myriastiches* and Upper Ordovician *Aulechinus* (which Mortensen considers as ancestral to later echinoids), as well as other morphological reasons, militate against *Bothriocidaris* being considered the ancestor of the echinoids or even being considered a member of the Class Echinoidea.

Mortensen further points out that the Paleozoic archaeocidarids and lepidocentrids have living descendants and that there is no sharp distinction between the Paleozoic and later echinoids. He also notes, although he does not recognize it in his classification, that the Irregular echinoids are derived from several, perhaps 3 or 4, sources among the Regular echinoids. Mortensen also indicates that the Order Camarodonta (and perhaps others) among the Regular Echinoids is polyphyletic and thus an unnatural group, although he continues to use it. These facts, as well as others not noted here, point to the need for a revision of the currently used major classification of the Echinoidea.

Of considerable significance is the establishment of the presence of growth lines (Durham, 1951; Zoeke, 1952) in the plates of several different kinds of echinoids (and presumably, therefore, in all). The growth lines show the changes in shape the plates have undergone during ontogeny, and inasmuch as they are complete and not interrupted in all cases observed, they appear to cast considerable doubt on the occurrence of resorbtion as a factor in growth and change of shape in the various plates of the test (however this is not evidence against the complete resorbtion of plates around the peristome).

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
V. *Mollusca: Pelecypoda*

By Norman D. Newell
The American Museum of Natural History
and Columbia University, New York

The pelecypods form a truly diverse group of invertebrates of great geological antiquity for which more than 7500 generic and subgeneric names have been proposed, some 2000 to 3000 of which may prove to be useful after elimination of homonyms, synonyms and unrecognizable categories.

Classification of the fossil forms involves special difficulties because knowledge of internal shell characters is required, especially details of the hinge and muscle insertions which generally are not clearly visible. The majority of pelecypod shells are, and apparently have always been, formed mainly of the unstable mineral aragonite, hence shell characters of examples from formations older than the Tertiary commonly are obscured or destroyed as a result of recrystallization, solution and other diagenetic changes. Therefore, an understanding of morphological details in the older pelecypods is dependent on exceptionally well-preserved specimens which are even more essential for the pelecypods than for other molluscs. For this, and for other reasons, existing classifications of pelecypods have not adequately taken into account the early geological history of the group, and many of the current views with respect to pelecypod taxonomy are only crude inferences based mainly or solely on comparative morphology of living forms and therefore are not applicable to the greater part of the history of the class.

Many diverse classifications of the bivalves have been proposed by both paleontologists and neontologists and each has stressed one or another line of evidence. None really has taken full advantage of existing knowledge.[1] Classifications in which higher categories are based primarily on soft anatomy have been some-

[1] Haas (1938) and Iredale (1939) have reviewed the voluminous literature on the most significant attempts to develop a satisfactory classification of the pelecypods.

what favored by zoologists as compared with those based on skeletal characters. It has frequently been assumed that muscles and organs are somehow more fundamental than skeletal parts, and hence are the best indicators of relationship. On the contrary, all lines of evidence must be considered, anatomy, morphology, ontogeny, and paleontology, and of these the evolutionary records of the stratigraphic succession provide, after all, the most valuable clues in the search for phylogeny. Although this will seem obvious nowadays to many systematists, there are still a few who are not acquainted with the richness of the fossil record and who are not impressed by the vastness of geologic time.

After the pioneer efforts of Linnaeus and Lamarck, the grouping of the bivalves followed expediency for many decades. Then, with remarkable insight, the great Viennese paleontologist, Neumayr, developed a comprehensive classification in 1883 based primarily on features of the pelecypod hinge (Neumayr, 1883, 1891). His conclusions soon gained wide recognition and adoption, partly because of Neumayr's great personal prestige, but even more because of the practical value of his results which have to some extent influenced all subsequent work on the group.

Six years after the appearance of Neumayr's first work on pelecypod systematics, Dall (1889) introduced an outline of his classification which was to prove influential, particularly in America. Fundamentally, his work, which was not fully developed until 1895 (Dall, 1895), was not radically different from that of the Austrian paleontologist, but it incorporated many improvements. Dall followed Neumayr's lead in emphasizing the importance of the pelecypod hinge in classification of the group. He also recognized the value of shell form and structure, adductor asymmetry, and development of siphons as taxonomically very significant. Unfortunately, he was somewhat intolerant of the pioneer contribution of Neumayr and he produced some confusion by the introduction of several new terms for approximately the same groups recognized in the earlier work. While Neumayr and Dall were working on pelecypod systematics, Pelseneer (1889), a French zoologist, proposed a wholly new classification in which the higher categories were based on details of gill structure, but unlike Neumayr and Dall he gave practically

no consideration to the succession of fossil forms and he relegated shell characters to a subordinate place among bases of classification. Consequently, his conclusions were at considerable variance with previous arrangements and they tended to bring together many dissimilar kinds of shells. This classification, with minor alterations, is still favored by a few neontologists, but a majority now use a somewhat uncritical and heterogeneous synthesis by Thiele (1934) of the works of Neumayr, Pelseneer, and Dall.

In 1895 Dall, considering the work of Neumayr and Pelseneer, arrived at a taxonomic arrangement which, with but little modification, is embodied in the final edition of the Eastman-Zittel Textbook of Paleontology published in 1913 and has been generally followed by American paleontologists. However, this classification, since it appeared half a century ago in essentially its final form, does not agree in many respects with the conclusions of many investigators about phylogeny.

The last really notable attempt to build a classification of pelecypods (founded on somewhat new lines) was that of Douvillé (1912). Douvillé was one of the leading paleontologists of the time and he made use of much more ample paleontological data than were available in the earlier efforts. Although very imperfect and incomplete, his classification represents a real advance and has been widely used by British and French paleontologists. Neumayr, Pelseneer, and Dall did not have access to sufficient data on the succession of pelecypod faunas to enable them to arrange their higher categories in a temporal sequence. Furthermore, none of these students displayed any considerable understanding of the principles of animal evolution. Their conclusions were based mainly on comparative morphology with only general recourse to the faunal sequence. In no sense were they based on phylogenetic analyses.

In his work on the pelecypods, Douvillé took advantage of the principle of adaptive radiation which already had become a basic aspect of vertebrate phylogeny. He also took into account valuable ontogenetic data worked out by the French paleontologist, Bernard (1895-1897), but generally not appreciated by other investigators. It is unfortunate that the American and German students of pelecypods have tended to overlook Douvillé's contribution.

The fundamental general studies over pelecypod taxonomy were mainly between 1889 and 1912, and later general classifications are based in one way or another on the earlier efforts; hence they are not really new. Since they do not make use of steadily accumulating paleontologic evidence, they do not represent very much progress toward an understanding of the general

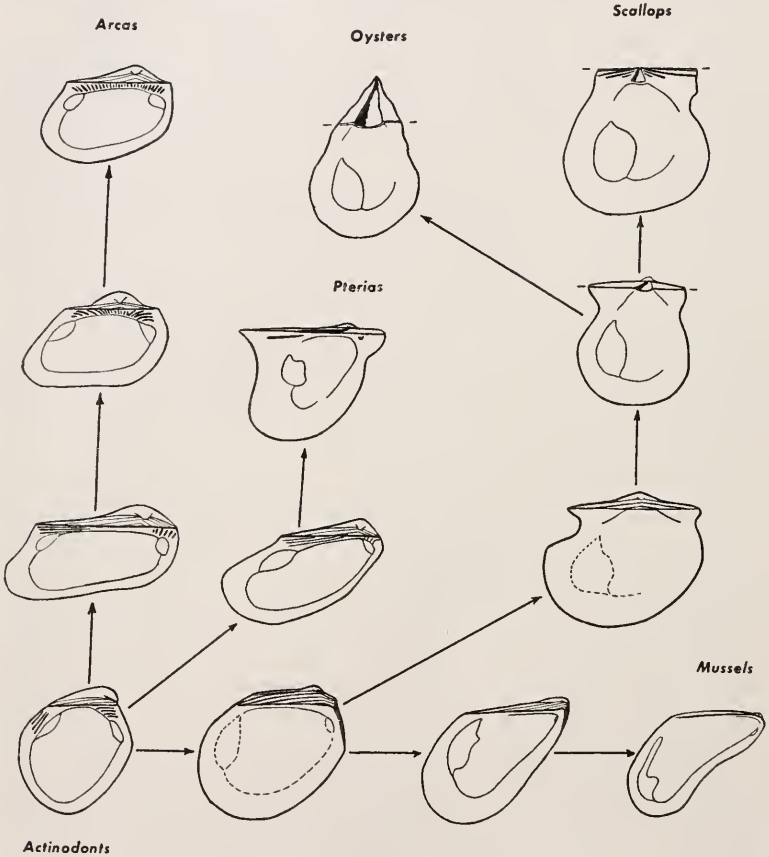

Fig. 1. Probable phylogeny of the Arcacean pelecypods and their anisomyanian relatives since the Ordovician period, illustrating marked parallelism in the development of hinge characters. This is the "sedentary" branch of Douvillé. Representation is generalized; particular genera are not intended.

phylogeny of the Pelecypoda. It now seems clear that the majority of existing families and superfamilies of pelecypods originated before the Jurassic period. The faunas of older times, although still poorly known, are much better understood today than they were in Douvillé's time, and it is probable that the origins of many of the higher categories will be worked out when available data on the older pelecypod faunas are evaluated.

Parallel evolution is common in the pelecypods where separate but related lines pass through closely similar morphological stages. Convergence between more distantly related groups is also a complicating factor which may result in an artificial association of basically unlike groups. Attention to the stratigraphic sequence of forms enables us in many cases to discriminate between convergent and parallel trends (Fig. 1). For example, some of the Recent Arcaceans possess taxodont dentition and because of this have been placed by most students close to the nuculoids. However, as pointed out by Douvillé, the Mesozoic and Paleozoic ancestors of the Arcaceans are not at all like the nuculoids. They possess a very different dentition of the type (cyrtodont-parallelodont) which characterizes many primitive Pteriaceans, Mytilaceans, and allied pelecypods. The taxodont dentition of the Recent Arcaceans represents a very late convergence toward the basically unlike nuculoids.

The Arcaceans and their ancestors possess a distinctive complex ligament type which I have termed duplivincular (Newell, 1937, 1942). This is found in living pelecypods only among Arcacea, and in the ancestry of Pteriaceans, scallops, and the marine mussels. In all but the Arcacea the duplivincular ligament was replaced before the Jurassic by other kinds of ligaments. Ligament evolution in these groups has followed parallel trends. In the majority of living Pteriidae the ligament is similar to that of living oysters, but as shown by the sequence of fossils, it was developed separately in the two lines from different ancestors that possessed the duplivincular ligament. This is a trend which has independently characterized several lineages.

Attention to ligament characteristics, almost completely ignored by pelecypod systematists in the past, promises to provide additional clues to phylogeny. For example, in both the pterioids and the scallops the ancestral duplivincular ligament is replaced

by a so-called external ligament possessing one or more resilia. In the former this change occurred during the Permian, in the latter during the Devonian. These grades of ligament structure, arrived at independently through selection and parallel adaptation,[1] certainly are useful in recognition of higher categories, but they may not be of equal value in different groups. The same applies to many other characters of pelecypods, among which may be enumerated the structure of gills, respiratory siphons, size and distribution of adductor muscles, possession of a byssus, shell microstructure, and dentition.

The experience of the majority of students since Neumayr has tended to confirm his conclusions with respect to the relative conservatism of pelecypod dentition, and the emphasis given hinge teeth and sockets in classification of pelecypods probably has been justified, even though other characteristics must also be given weight. Independent development in separate stocks of closely similar dentitions, as in the Nuculaceans and Arcaceans cited above, probably is not common and in any case can be evaluated by reference to the temporal sequence of forms.

The teeth and sockets of the pelecypod hinge lie below the hinge axis. They do not serve as fulcral points, hence they are not closely analogous to similar convergent structures in brachiopods and ostracodes. Their main function in pelecypods is to guide the valves as they close so that they will always fit snugly at the margins. Obviously a good marginal fit between the valves is of high selection value in those pelecypods that are not buried and protected by the substratum.

R. Anthony (1905) has shown that the position of the hinge axis within the ligament is not permanently fixed. By means of a smoked paper and a stylus cemented to one valve of a living pelecypod (Fig. 2), he was enabled to record the successive, often erratic, wandering of the hinge axis during opening and closing of the valves. In the first two examples of Figure 2, dental articulation is loose and the ligament flexible, hence the valves deviate laterally in the sagittal plane. These forms normally are burrowers so that a truly efficient hinge is not needed. In the other

[1] E. R. Trueman, who is systematically investigating pelecypod ligaments, has shown experimentally that there is a direct correlation between mechanical efficiency of the ligament and the mode of life (Trueman, 1953). Hence it seems practically certain that variations in ligament structure are adaptive and that the observed evolutionary trends in ligaments are also adaptive.

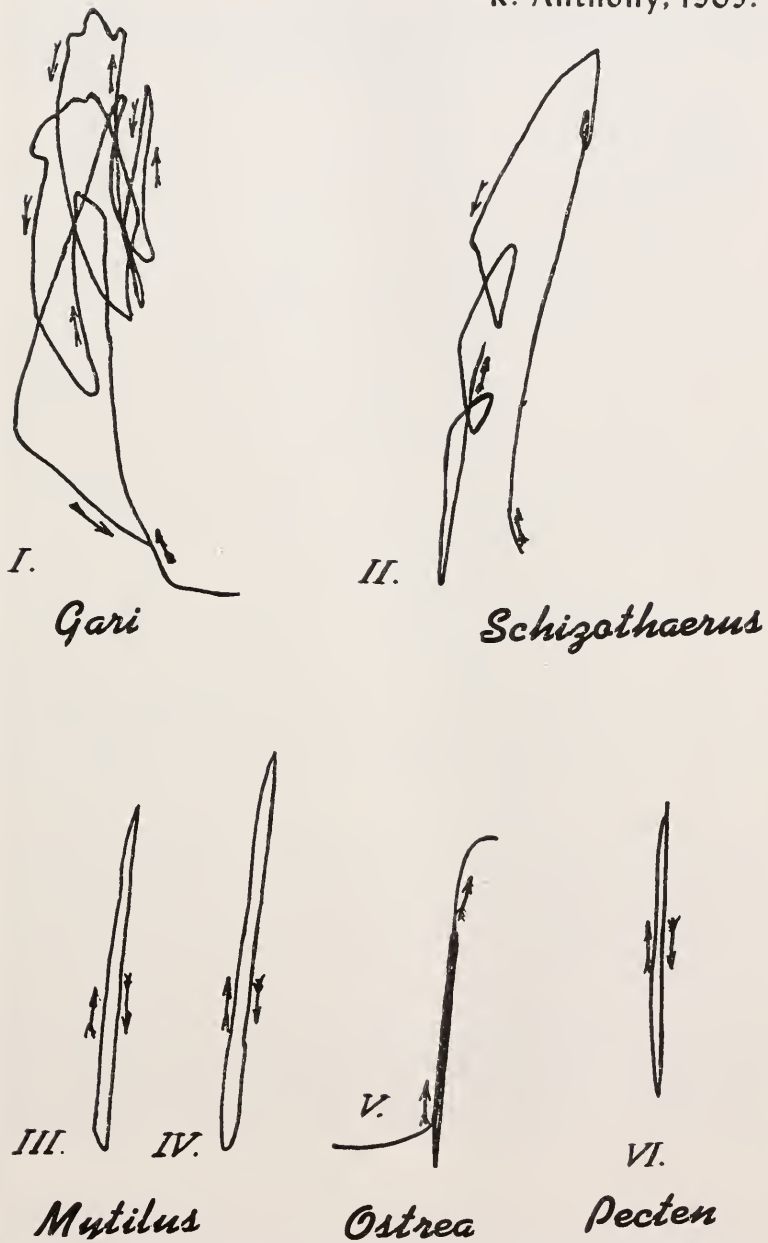

Fig. 2. Erratic migration of hinge axis within the ligament during opening and closing the valves in some living pelecypods. (Modified from Anthony.)

examples, even though teeth and sockets are poorly developed or lacking, the ligament is sufficiently strong and efficient to prevent lateral slippage of the valves and displacement of the axis of motion. Additional experimental evidence might be sought, but it seems clear that the function of the teeth and sockets is to supplement the ligament which is the true hinge. Adaptation to mechanical stresses in different lines has resulted in the observed multiplicity of dental patterns and ligament types, which together make up the hinge complex of the pelecypods.

Examination of the record of fossil pelecypods shows that many groups exhibit a strong "family resemblance" in general expression, and it is on these general resemblances that many of the families and superfamilies of existing classifications rest. In some cases the categories so distinguished seem to be natural units. For example, the oysters and their near relatives, which became clearly separate in the Triassic, comprise a compact and well-defined group. The Pteriaceans, comprising somewhat less distinctive groups with very ancient origins (in the Ordovician), almost certainly are polyphyletic. The Trigonias clearly are a separate line as far back as the Devonian, beyond which the evidence is obscure. The scallops likewise form a major adaptive group which is quite distinctive in general expression. It can readily be followed back into the Silurian (Newell, 1938). However, in all of these groups there was considerable progressive evolution in hinge characters and in composition and microstructure of the shell. These evolutionary changes have provided the criteria by which families, genera and species are recognized. The faunal sequence suggests that the true scallops probably are monophyletic if we exclude the Amussiidae (Pernopecten) and Limas which were independent long before (Devonian) the Pectinidae appeared in the Triassic. In terms of morphologic distinctness and separation for hundreds of millions of years, there are sound arguments for recognition here of at least three major categories.

The conclusion that can be drawn from the literature on pelecypods is that several classifications in use tend to stress different characters and are not in general agreement. Furthermore, none is in harmony with the known facts of the paleontological succession, and to this extent certainly they cannot be regarded as

phylogenetic. In general, the relationships among the higher categories have not been subjected to extended inquiry in the past 40 years, and insufficient attention has been given to rather widespread parallel tendencies in evolution.

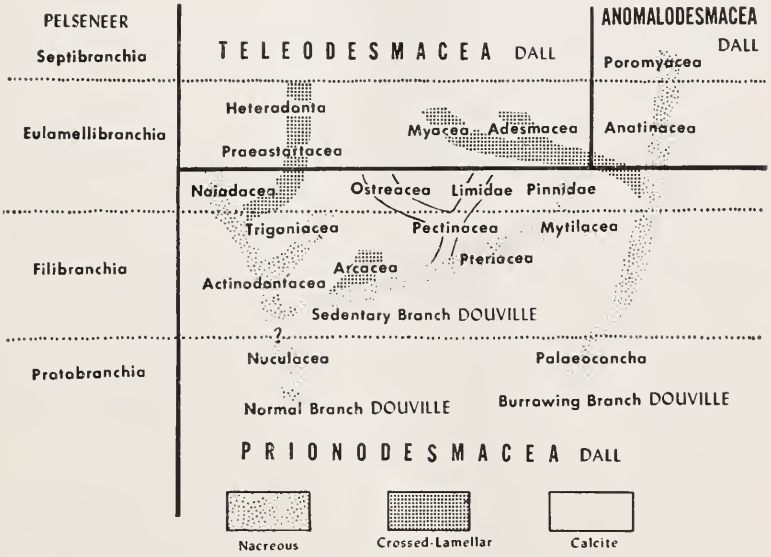

Fig. 3. Diagrammatic representation of bivalve classifications of Pelseneer, Dall, and Douvillé. Douvillé's arrangement, although subject to many improvements, in some respects corresponds more closely to the evidence of fossil succession than do the others. (Modified from Davies.)

The chart of Figure 3, modified from G. Morley Davies (1933), is an oversimplified comparison of the taxonomic schemes of Pelseneer, Dall, and Douvillé, all of whom have borrowed from Neumayr. Superimposed on this is shown the taxonomic distribution of a few kinds of shell structure. In Pelseneer's classification, four orders are recognized based chiefly on gill types. Since a single gill type is found in quite dissimilar animals (Fig. 3), and different types of gills in groups which on structural and paleontological grounds seem to be homogeneous, it seems clear that modifications of the gills have followed a simple adaptive trend.

Elaboration of the microscopic structure of the shell seems also to have followed a characteristic trend observable in several groups. Students of molluscs generally are agreed that nacreous structure is a primitive character. The so-called porcellanous (crossed-lamellar) structure, as pointed out by Dall, characterizes the more specialized members of each major group with an outstanding exception, the Arcacea, which although primitive in most respects, possess crossed-lamellar shells (Fig. 3). Dominantly calcite shells are found in only post-Paleozoic Limas, oysters and scallops which on most counts seem to be closely related. As shown elsewhere (Newell, 1937), the Paleozoic scallops possessed both nacreous and crossed-lamellar shells unknown in Recent forms. On the other hand, calcite shells, characteristic of modern scallops, are unknown in the Paleozoic forms. It seems that crossed-lamellar shells have developed several times in the pelecypods from nacreous shells.[1] The use of calcite throughout is clearly a mark of specialization in this group and probably was achieved more than once. For example, the most probable Paleozoic ancestors of oysters (Pseudomonotinae) and scallops (Aviculopectininae) had diverged widely during the Permian period but had not yet acquired calcite shells.

Dall based his three orders mainly on types of dentition, but he tried also to equate other lines of evidence. Douvillé was able to correct a few of the more outstanding errors of Dall's classification; for example, the unnatural association of the Arcaceans and Nuculaceans. He separated three major groups according to general mode of life. One of these includes most (but not all) of the byssate and heteromyarian forms under a so-called fixed or sedentary branch. The majority (but not all) of the burrowing forms, provided with siphons and a weak hinge, form a second division and all other pelecypods were placed in his "normal branch". It is now clear from the fossil record that the sedentary branch of Douvillé in broad outline constitutes a natural group (Fig. 1), although it cannot be simply defined in terms of gill structure, hinge characters, or shell structure. The other two branches probably are polyphyletic.

Obviously, comparative morphology of living forms alone cannot give us a phyletic classification. The matter will not be

[1] Probably this has also occurred in the gastropods where crossed-lamellar shells are regarded as an indication of specialization.

resolved until succession in time of the fossil forms is understood and given very high rank among the various lines of evidence.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
V. *Mollusca: Gastropoda*[1]

By J. Brookes Knight[2], Roger L. Batten[3], and
Ellis L. Yochelson[4]

During the past several years, Dr. J. Brookes Knight, with the junior authors, has been studying the morphology and systematics of the Paleozoic gastropods for the Treatise on Invertebrate Paleontology. Recently we have spent some months in an effort to integrate systematically our findings on Paleozoic genera with those of other workers on post-Paleozoic forms. From these studies we have constructed a classification that embodies ideas and principles taken from an examination of living and fossil gastropods. This classification, given in Figure 1, is still tentative, and its full meaning will not become evident until the families and genera in the superfamilies are given in the completed Treatise.

We have used the anatomy of the soft parts as the basis for constructing this classification. By coordinating information about the anatomy of living forms and their shell features, it has been possible to make an estimate of the probable soft anatomy of many fossil gastropods — at least in broad outline. Actually the shell can be brought to yield, with a reasonable degree of probability, much more anatomical information than has been generally thought. If applied with due consideration for the order in which animals appear in time, for ecological differences, and for similarities due to convergence, inferences based on this information lead to results in classification that seem more plausible than those constructed by using other methods. Of course, like all attempts at phylogenetic classification this one is hypothetical, and additional information or different interpretations may later alter it.

[1] Publication authorized by the Secretary of the Smithsonian Institution and the Director, U. S. Geological Survey.
[2] Research Associate, Smithsonian Institution, Washington 25, D. C.
[3] Columbia University, New York, New York.
[4] Geologist, U. S. Geological Survey, Washington 25, D. C.

From the time of Lamarck, the construction of phylogenies and classifications was chiefly the work of neontologists. They based most of their conclusions on studies of the comparative anatomy of a relatively few living species. Much of their interest

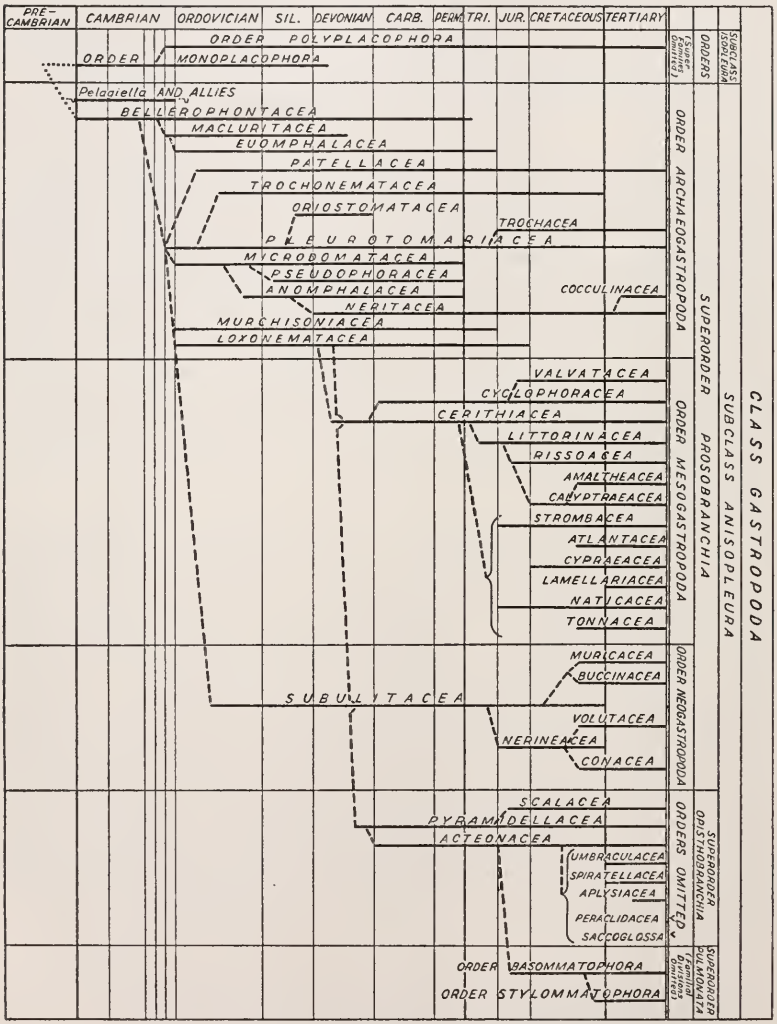

Fig. 1. Proposed phylogeny of the Gastropoda.

was concentrated in the attempt to discover missing links and to construct hypothetical ancestral types, all with little attention to or understanding of fossils.

Paleontologists, on the other hand, busy describing genera and species, were seldom concerned with supra-familial categories and were content to have their fossils placed in divisions erected for living species. Paleozoic gastropods suffered the most from this haphazard treatment because they differ most from the living forms. Mesozoic species were generally classified more rationally. Those of Cenozoic age, which differ little from those living today, were for the most part correctly classified but placed without roots into the past.

The great difference in Paleozoic gastropods as compared with living ones can be seen by observing the distribution of the major categories in time as shown in Figure 1. Note the concentration of Archaeogastropoda in the Paleozoic era and the Mesogastropoda and Neogastropoda together with the Opisthobranchia and Pulmonata in the late Mesozoic and Cenozoic eras.

It has only been within the past decade that sufficient information about the anatomy, embryology, and physiology of critical living species has been available. This information combined with previous observations — and above all with a deeper understanding of the more ancient fossils — has made possible the recognition of the probable ancestral groups of the major ordinal categories and some understanding of the evolution among them.

Let us turn to an example of what can be done by correlating the anatomy of the soft parts with conchology. Among the Monoplacophora, which range from early Cambrian to Devonian, is a group of cap-shaped shells, the Tryblidiidae. For many years they were considered to be primitive patellids, which they do resemble superficially in shape. In 1938, Wenz made the suggestion that those ancient forms were actually very primitive bilaterally symmetrical animals. He based this idea on the presence of symmetrically paired dorsal muscle scars as contrasted with the horseshoe-shaped muscle scar of the patellid shell. If Wenz was correct, as we believe he was, it follows that these primitive forms did not undergo torsion of the soft parts as do the patellids but were quite similar in internal organization to the chitons (Polyplacophora).

This was a revolutionary idea in gastropod systematics. It was arrived at by discounting superficial shell resemblances and concentrating on what might be learned from the record of the soft parts that was preserved in the shell. In this case it was merely the scars left by the pedal muscles, but it was enough to give a clue to the probable internal anatomy of monoplacophorans. The cap-shaped shell of *Patella* and patellid like forms has been achieved by many unrelated rock-clinging gastropods; it is most often an ecological adaptation and does not necessarily point to relationships. Unfortunately, except in cap-shaped shells, muscle scars are extremely difficult to observe, even in Recent gastropods.

Other features in the shell often correlate with specific features of the anatomy. One of the most important shell features that can be correlated with anatomical characters is the emargination or channel that marks the position of the anal tube. Since the ctenidia (primary gills) and other pallial organs have fairly definite relationships to the position of the anus, this may give information as to whether there was the primitive pair of gills or only a single gill. An anterior canal or notch accompanied by certain related features commonly indicates an inhalent siphon. A heterostrophic nucleus has been shown to characterize certain opisthobranchs inhabiting the present-day plankton. These examples indicate the type of inferential data that is important in the estimation of the anatomy of extinct gastropods.

If we then reconstruct the soft anatomy of our early gastropods inferentially, we can discuss their probable evolution in terms of three principal adjustments: flexibility in the Isopleura and increased motility and enhanced sanitation in the Anisopleura.

To return to the monoplacophoran, we have inferred that it had the anatomy of a bilaterally symmetrical organism, much like that of the chiton. The major evolutionary advance within the Isopleura was the replacement of the single monoplacophoran shell by a series of eight transverse plates. This gave the animal greater flexibility and permitted it to cling closer to the irregular surfaces of the rocks. So successful was this adjustment to its narrow environment that the chitons, appearing for the first time in the late Cambrian, survive today with very little change and virtually no adaptive radiation.

It may be appropriate to say at this point that most zoologists

who are unfamiliar with the fossil record and who may not be aware of the existence of the Monoplacophora regard the chitons as a separate class reflecting characters of the ancestors of the gastropods, if not all mollusks. As paleontologists we prefer to be guided by the fossil record and suggest the Monoplacophora for the ancestral role. Whether the Isopleura be regarded as a subclass or a separate class from the Anisopleura is relatively unimportant; if the current separation is maintained, we feel that the Monoplacophora should be included with the chitons (see Figure 1).

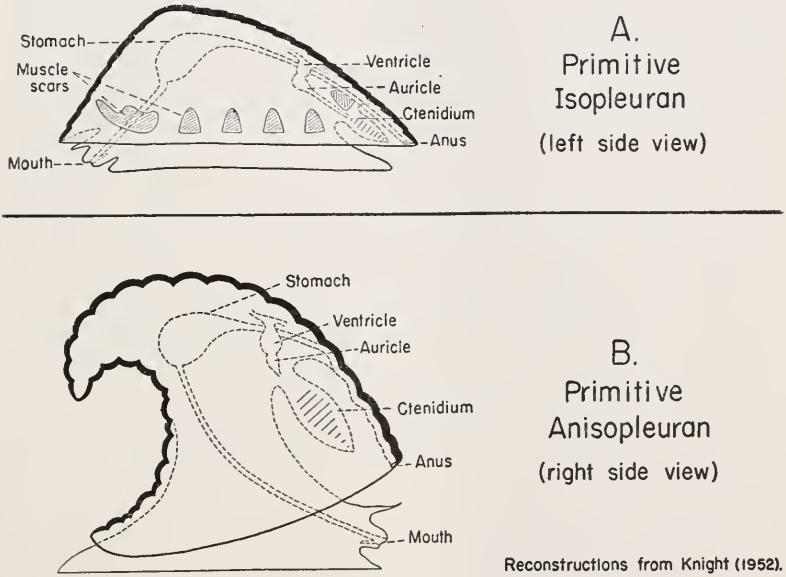

Fig. 2. Schematic reconstructions of two gastropods.

The introduction of the phenomenon of torsion gave rise to the Anisopleura with greatly increased motility and a newly important problem of sanitation. Figure 2A represents the left side of a primitive monoplacophoran restored with an organization similar to that of a chiton, shown with the shell transparent. Note that the anus lies in a posterior mantle cavity between a pair of ctenidia. As in the chiton, the posterior position of the anus obviates the need of any elaborate provisions for sanitation. Note

also that the broad, low shell with its equally broad, low foot and its rather complex muscle attachment, permit little movement of the shell and probably allowed only very sluggish progression.

Figure 2B represents a restoration of a gastropod-like mollusk of the early Cambrian that is thought to be a primitive bellerophont, an advanced, relatively tall monoplacophoran, so to speak, that has undergone torsion. This is a view of the right side and is also drawn as being transparent. As is well known, torsion takes place in an early stage of the trochophore larva. This torsion occurs in such a way that the primitively posterior mantle cavity, with the anus lying between a pair of ctenidia, develops in a forward position over the head, just as if the shell with the visceral hump and contained organs had been twisted 180° in a counterclockwise direction relative to the head and foot.

Note that the broad, low shell in Figure 2A has become an elevated one with the curvature that must have initiated coiling. The elevated shell may have provided for a long, slender neck such as that possessed by most living Anisopleura, which — combined with the reduction of the shell muscles to a single pair — would have permitted free movement of the shell relative to the foot. The anterior mantle cavity now permits the withdrawal of the body headfirst into the shell. Surely the traditionally slow-moving snail has become an active race horse as compared with the probably almost stationary monoplacophoran.

But the problem of keeping the ctenidia free from fecal matter is now more difficult. Let us now consider briefly the series of solutions that gave those gastropods which possessed them competitive advantage.

The first solution was the development of an anal emargination (a sinus or slit) for the egress of fouled ciliary currents without contaminating the ctenidia that lay on each side. This solution was used by the bellerophonts and pleurotomarians. Next — after the introduction of asymmetrical coiling — came the suppression of the right-hand ctenidium and associated organs. As a result the ciliary currents entered the mantle cavity from the left anterior side and departed by the right posterior immediately after passing over the anus, which had migrated to that position after the loss of the right ctenidium. Such a development occurred several times within the archaeogastropods and led to the

origin of other orders. Still further adaptations, also leading in part to the origin of new orders, were the gradual return of the anus to a posterior position in the adult of many opisthobranchs and — the last step — loss of the shell with almost full bilateral symmetry in the adult.

A final adjustment not discussed here is the adaptation for life on the land with conversion of the mantle cavity into a lung and the loss of ctenidia in the pulmonates.

In summary, this classification shows that while the living Isopleura have undergone very little change since late Cambrian time, the Anisopleura have radiated outward to become one of the most successful animal groups. Living snails have become extremely numerous and varied and have invaded all habitats and all environments from high mountains to the depths of the oceans.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
V. *Mollusca: Cephalopoda*

By Bernhard Kummel
Museum of Comparative Zoology, Cambridge, Mass.

Few invertebrate classes possess (or are plagued with) the volume of literature and diversity of interpretation, or are so susceptible as media of philosophical speculation as the fossil cephalopods. A complete review of the literature and progress in the study of fossil cephalopods is beyond the scope of this paper. Therefore I will center attention on the geologic distribution of fossil cephalopods and current ideas on classification and evolution. The extent and degree of cooperation towards a uniformity of nomenclature — both morphological and taxonomic — that has prevailed in the past few years among the European and American authors responsible for the Cephalopoda for the Treatise has been truly inspiring. The results of this labor will place the study of these animals on a new threshold. It is a pleasure to acknowledge the data on Jurassic ammonoids furnished by W. J. Arkell; the data on Cretaceous ammonoids furnished by C. W. Wright; the data on Paleozoic ammonoids furnished by A. K. Miller; the data on the Dibranchiata furnished by L. Bairstow; and data on nautiloid genera by Curt Teichert. Of the three major groups of Cephalopoda, I will confine most of my remarks to the Ammonoidea. Recent tabulations indicate that there are approximately 3000 valid genera of fossil cephalopods with more than an additional thousand generic names which go into synonomy.

Within the Nautiloidea there are now recognized approximately 700 genera. Their evolutionary pattern is one of intense radiation in the Ordovician during the initial phases of their evolution, followed by a rapid and steady decline until the present day with our one remaining relic genus. The main pattern of distribution of nautiloid genera as illustrated on Figure 1 has been known for a long time. Morphologically the nautiloids are a highly diversified group but many of the orders that made their

appearance in the Ordovician became extinct by the Silurian and Devonian. During the latter half of the Paleozoic the evolutionary rate of the nautiloids was greatly diminished. A second surge occurred in the Upper Triassic which has a diversified nautiloid

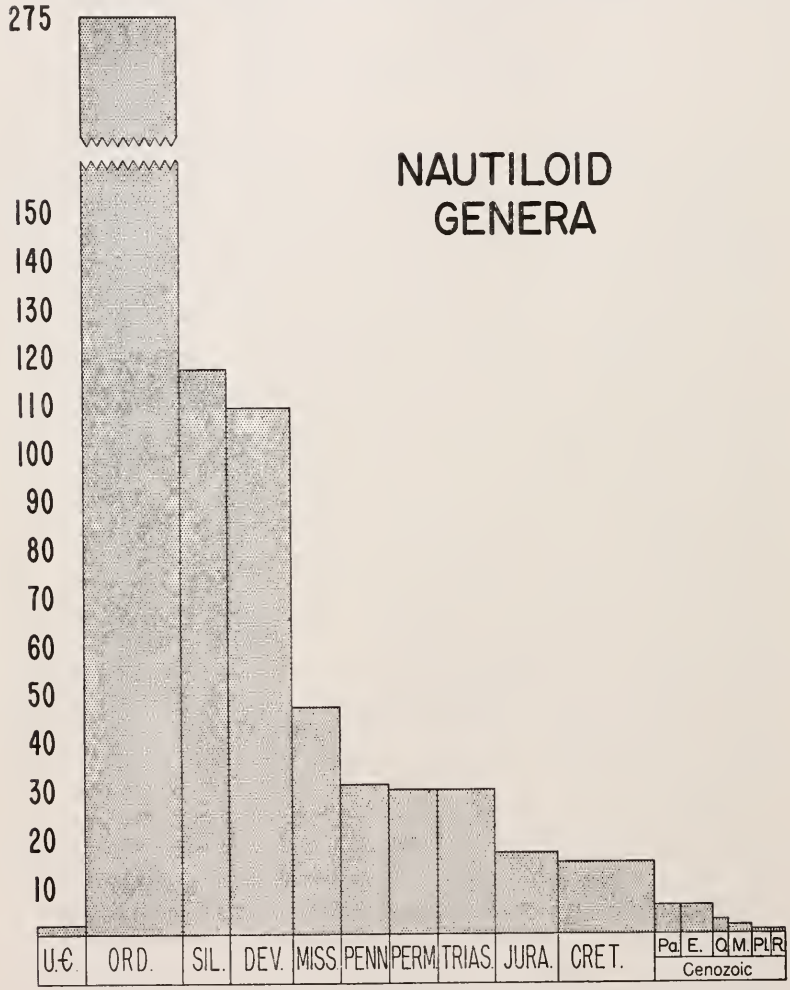

Fig. 1. Bar graph showing number of nautiloid genera in each geologic period. (Data from C. Teichert, personal communication.)

fauna, but nothing compared to that of the early Paleozoic. The evolutionary pattern of the nautiloids in the Triassic is merely a culmination of trends begun back in the Carboniferous. The Permian was not a period of crisis for the nautiloids as it was for the ammonoids, but in the late Triassic (Rhaetian) there was almost complete extinction of the nautiloids. No Rhaetian nautiloids are known, but a single specimen from the Carnian of New Zealand offers strong evidence that an offshoot of the Syringonautilidae survived into the Lias (Spath, 1927, p. 23; Kummel, 1953); from this family all post-Triassic nautiloids are derived. The Jurassic to Recent history of the nautiloids duplicates the general pattern shown by the Paleozoic forms; that is, there is an initial experimental phase of extensive radiation from which arose several more stable stocks, none of which, however, was long lived. In the Cenozoic only three new genera appear, of which only *Nautilus* survives.

Up until recently the classification of nautiloids has been completely dominated by the scheme proposed by Hyatt in the 1900 edition of the Zittel-Eastman Textbook of Paleontology. Today there is no doubt in anyone's mind that Hyatt's scheme is untenable. The rejection of Hyatt's classification is the rejection of a systematic arrangement based on a single character. The tentative scheme recently proposed by Flower and Kummel (1950) summarizing existing thinking can unquestionably be improved but it has had the very desirable effect of crystallizing attention on the more critical problems. There is wide agreement among nautiloid specialists that the number of orders proposed by Flower and Kummel should be reduced, but no agreement as yet as to how this should be done. Of the 13 orders recognized by these authors the Ellesmeroceratida, Endoceratida, Michelinoceratida, Ascoceratida, Discosorida, and Oncoceratida are generally accepted as well defined groups and appear to need only minor revisions. The recognition of an Upper Triassic *Bisiphytes* (Family Nautilidae) which shows clear affinities to the Syringonautilidae changes the derivation of all post-Triassic nautiloids to the Triassic Syringonautilidae rather than the Paranautilidae as previously proposed (Kummel, 1953). This change necessitates the suppression of the Centroceratida and the joining of these families into the Nautilida. The Rutoceratida can most

probably also be included in the Nautilida but clear evidence of this relationship is not available (R. H. Flower, personal communication). Flower (1952) would derive the Rutoceratida from the Oncoceratida. The Liroceratidae, Ephippioceratidae, Paranautilidae, Clydonautilidae, and Gonionautilidae, all formerly placed in the Nautilida, may now need to be placed in a new order. At first it would seem that they would be logically included in the Barrandeoceratida; however, connecting forms from the Devonian have not been recognized as yet. The status of the Solenochilida, Tarphyceratida, Barrandeoceratida, and Basslerocerati da is a source of disagreement among specialists. The crux of the difficulties and confusion in nautiloid systematics and evolution lies in the great host of early Paleozoic families. Taxonomic stability of these forms will be approached as our knowledge and understanding of their complex morphology and modes of adaptation is increased. Agreement on the systematics of early Paleozoic nautiloids is near but is not quite yet a reality. Because of this no phylogenetic chart is presented.

It is significant to note that in the past few years very few new genera have been established in spite of the fact that several large new faunas have been described. It would be pleasant to think that possibly we are near the limit of the total number of genera in this order. This observation is encouraging in that maybe now more effort and thought can be concentrated on critical paleobiological problems.

Ever since William Smith's great discovery of the usefulness of fossils for correlation and geochronology, the ammonites have played a leading role as a stratigraphic tool. The pioneer work of d'Orbigny, Oppel, Quenstedt, Mojsisovics, Waagen, Neumayr and many others firmly established the ammonites as the leading actor in the drama of Mesozoic stratigraphy. Likewise the nature of the ammonoid shell and its manner of growth has lent itself beautifully to the pliable minds of evolutionary theorizers. Few people have had more influence on the study of fossil cephalopods than Alpheus Hyatt whose whole philosophy revolved around the recapitulation doctrine — a principle not accepted today by most cephalopod students. However, few text books of zoology or geology fail to illustrate some of Hyatt's cephalopods demonstrating recapitulation in action.

The recent taxonomic house cleaning of ammonoid genera enables the construction of the bar graph (Figure 2) on the geologic distribution of ammonoid genera. There is a total of approximately 1800 genera of ammonoids; of these 172 are from

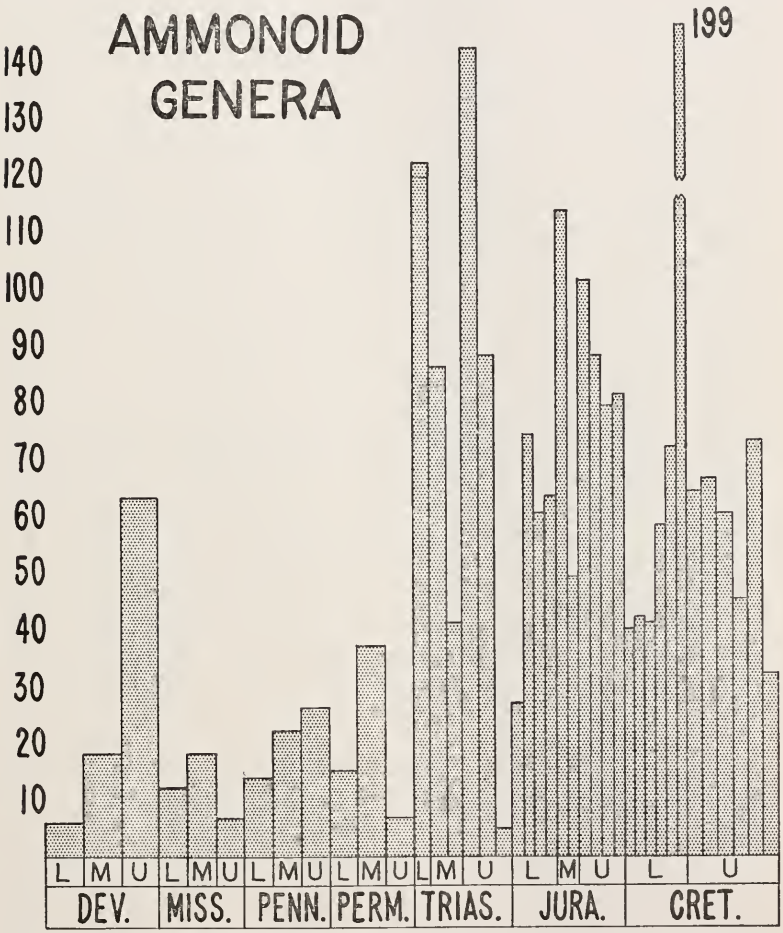

Fig. 2. Bar graph showing number of ammonoid genera in each geologic period. (Data on Paleozoic ammonoids from A. K. Miller, that on Jurassic ammonoids from W. J. Arkell, and that on Cretaceous ammonoids from C. W. Wright, personal communications.)

the Paleozoic, 370 from the Triassic, 735 from the Jurassic and 493 from the Cretaceous. There are an additional 1000 generic names that fall into synonomy. The largest number of these involve Jurassic ammonites.

The overall distribution of genera confirm commonly held views. In spite of specific instances of "monographic highs" and lack of record, it is the opinion of the Treatise ammonoid authors that the data reasonably reflect the history of this group of animals. In fact, C. W. Wright (personal communication), who compiled the list of Cretaceous ammonites, found his data most illuminating as a commentary on the validity of the Cretaceous stages. The most unusual aspects of the evolutionary history of the ammonoids are the three periods of crisis; during the first two such crises the group nearly became extinct and from but few surviving stocks even larger radiations developed until the final extinction of the group in the late Cretaceous. The two earlier periods of crisis are in the late Permian and in the late Triassic.

Several important aspects in the history of the study of ammonoids have greatly influenced our interpretation of ammonoid phylogeny and taxonomy. It is indeed remarkable that not until the 1860's did the splitting of the genus *Ammonites* really begin. The recognition of generic categories among the ammonoids developed rapidly after that date. Since this early period there have been proposed many taxonomic schemes for the Ammonoidea. Most of these, however, were based on a single character; the suture, sculpture, siphuncle, and length of body chamber have all been used in various manners with little success. Unit systems of classification invariably ended up by bringing together heterochronous homeomorphs.

Present interpretation of the relationships of Permian and Triassic ammonoids illustrates this point well. Figure 3 is a bar graph of total genera and new genera (dark stipple) of Permian and Triassic ammonoids. The average evolutionary tempo of Permian ammonoids is only slightly higher than that of the Carboniferous. The most striking feature is the presence of only seven genera in the Upper Permian. It should be kept in mind that the number of known fossiliferous Upper Permian deposits is indeed few. The ammonoid faunas of such classic areas as the

Salt Range, Djulfa, Timor, the Alps, Madagascar, and East Greenland are not abundant. The radiation of the ammonoids in the Lower Triassic is well demonstrated with its 128 genera. This radiation was not a sudden affair. Lowermost Triassic deposits, that is, those of Otoceratan age, are as scarce as marine Upper Permian strata. The smaller bar graph of Figure 3 shows the total genera and new genera for the six ages of the Lower Triassic. Only one genus carries on into the Triassic from the Upper Permian. It is not until the middle Scythian that a really large diversified fauna is encountered.

Figure 4 is a diagrammatic interpretation of the phylogenetic relationships of Permian and Triassic ammonoids. Of the two main groups of Paleozoic ammonoids, the goniatitids are represented by seven families in the Permian and the prolecanitids by five families. It has long been thought that many Middle and Upper Triassic ammonoids had their ancestry among these goniatitid families. However, the extensive researches of L. F. Spath over the past 30 years have demonstrated in a convincing manner the improbability of any of these goniatitid families being ancestral to any Triassic stocks. There are numerous cases of homeomorphy between many of these goniatitid genera and Middle and Upper Triassic genera. Permian ammonoids of the prolecanitid stock are included in two superfamilies. One of these — the Pronoritaceae — continues into the Triassic with a very modest development but did not give rise to any new stock. The ancestry of Triassic ammonoids is to be found in the Xenodiscaceae.

The most common and abundant lowermost Triassic ammonoids are the ophiceratids which show a wide range of variability in conch form. From this extremely variable ophiceratid stock arose directly or indirectly more than a dozen families of Lower Triassic ammonoids. This radiation is a continuation of that started at the base of the Triassic with the ophiceratids, and represents the height of the experimental phase in the eruptive comeback of the ammonoids after their near extinction in the late Permian. Most of the genera and families of this eruptive phase are short-lived but from a few of them arose the eight long-lived superfamilies that include most of the Middle and Upper Triassic ammonoids. Thus with the Anisian begins the stabilized phase in the evolutionary history of Triassic ammonoids.

The great decline and near extinction of the ammonoids in the Rhaetian has been known for a long time. From a peak of 140 genera in the Carnian there are left only a few species of 5 genera in the Rhaetian. There is a sharp decline in evolutionary development already in the Norian.

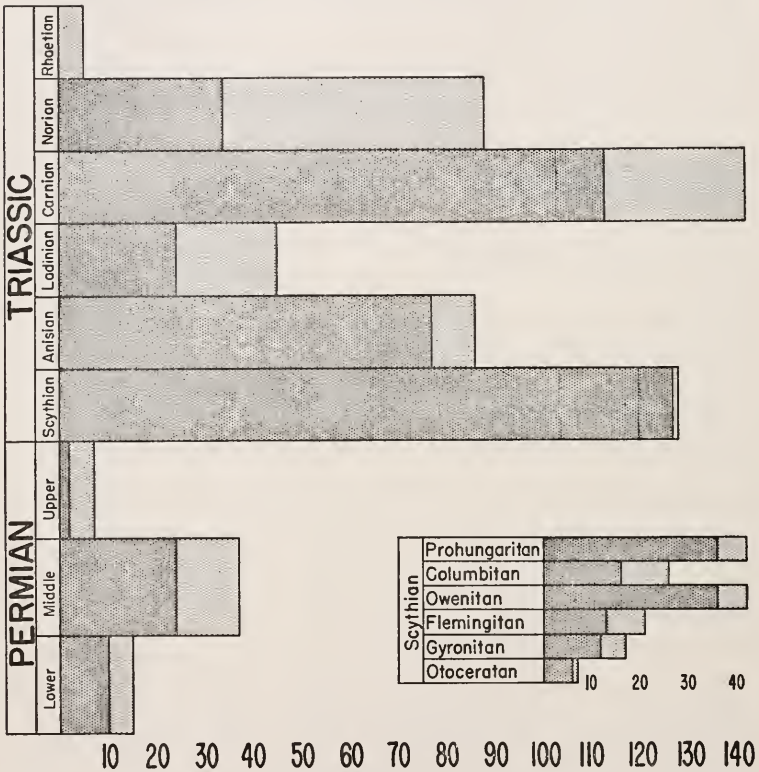

Fig. 3. Bar graph showing total number of ammonoid genera and new genera (dark stipple) in each stage of the Permian and Triassic.

A single stock carries through into the Lias to give rise to the great host of Jurassic and Cretaceous ammonoids. The evolutionary patterns of the ammonoids in these two periods is quite unlike that in the Paleozoic or Triassic. Two persisting, slowly evolving, root-stocks — the Lytoceratina and the Phylloceratina

— are the evolutionary reservoirs from which the great host of Jurassic and Cretaceous ammonoids are derived. The Lytoceratina and Phylloceratina are characteristic of the ancient Tethys; they are the leiostracous or smooth shelled forms. The trachyostracous or ornamented genera are most abundant in the epicon-

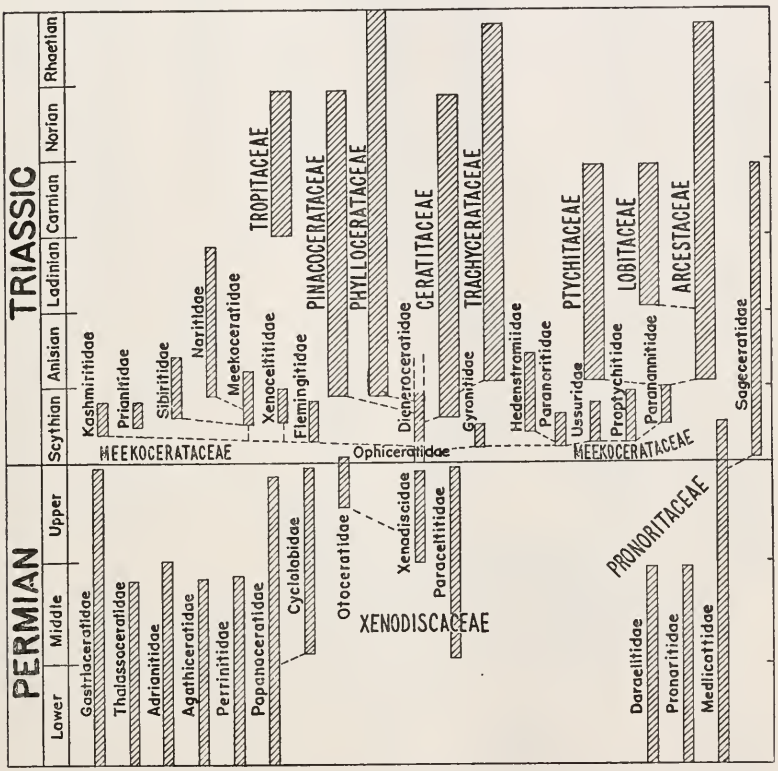

Fig. 4. Diagram showing inferred phylogeny and geologic distribution of Permian and Triassic ammonoids.

tinental seas adjoining the Tethys. Some 30 years ago Salfeld proposed his theory of Iterative Evolution in which he interpreted the innumerable throngs of the Ammonitina as arising through repeated radiations of offshoots from the conservative

stocks. Deciphering the countless threads connecting the Ammonitina and these conservative stocks is still evasive. More

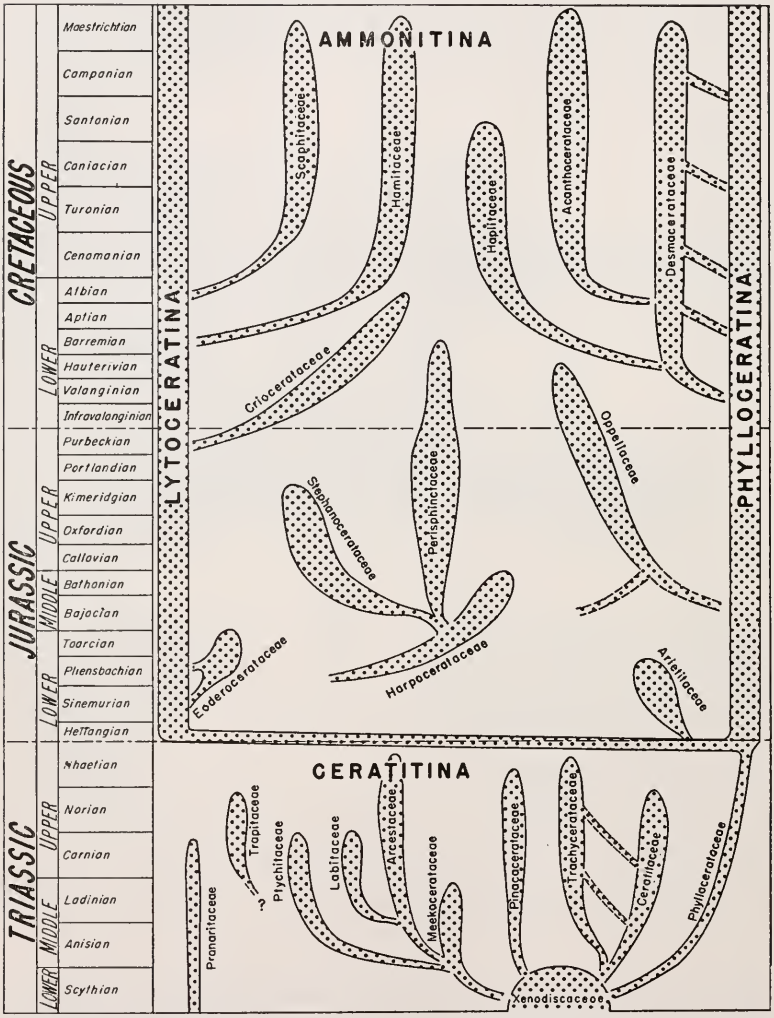

Fig. 5. Diagram showing inferred phylogeny and geologic distribution of Mesozoic ammonoids. (Adapted from Arkell 1950, Wright 1952, and Kummel 1952).

progress has been made with Cretaceous ammonites than with those of the Jurassic. When and if the various Jurassic and Cretaceous superfamilies can be more definitely tied to one or the other of the conservative root-stocks there will be need for modification of the suborder Ammonitina.

The Dibranchiata cephalopods have not received as wide attention as the nautiloids and ammonoids. Mr. Leslie Bairstow kindly furnished tentative and approximate data on the time

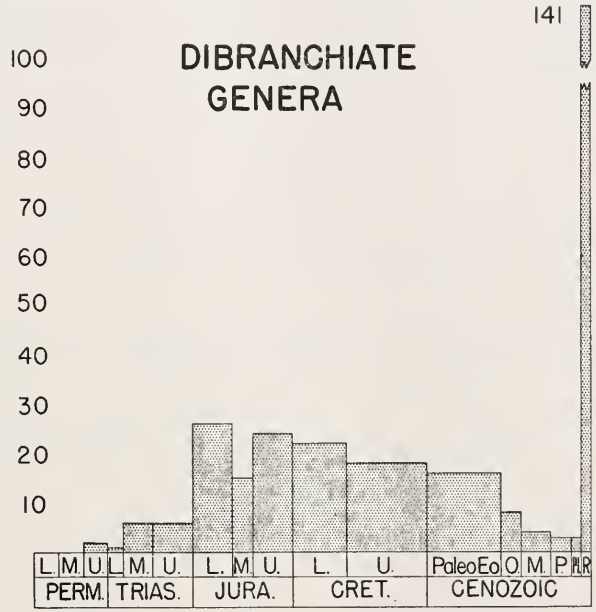

Fig. 6. Bar graph showing number of dibranch genera in each geologic period. (Data from L. Bairstow, personal communication.)

distribution of genera of Dibranchiata. The most striking feature of the bar diagram of Figure 6 is the great number of Recent genera; of the approximately 250 genera of Dibranchiata, 138 are known only from the Recent. The great diversity of Recent fauna, and the fact that many of the genera are very different from the nearest fossil forms known, imply the previous existence of many genera that are not actually known as fossils (L. Bairstow, personal communication). The incompleteness of the fossil

record of the dibranchs does not make them a suitable group for the study of evolutionary rates.

The present status of our knowledge of the fossil Cephalopoda presents an encouraging framework to direct and guide future research. The great success to which the cephalopods, especially ammonoids, have been used in stratigraphy has resulted in the major emphasis being placed on them as "tools" of stratigraphy. It is becoming more and more clear that a greater understanding of the animal and its ecology and adaptive range will add greatly to the value of the Cephalopoda as "tools" of stratigraphy and as "tools" for study of evolutionary processes.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
VI. *Arthropoda: Trilobita*

By Harry B. Whittington
Museum of Comparative Zoology, Cambridge, Mass.

The following notes express my own views and some that W. R. Evitt and I have developed jointly, and are not necessarily those of others working on Trilobita for the Treatise of Invertebrate Paleontology. I acknowledge with thanks the helpful discussions I have had with many friends, especially Drs. A. R. Palmer, C. Poulsen, F. Rasetti, and C. J. Stubblefield.

Many articles have been written on the classification of trilobites, but there is still no satisfactory arrangement. Major difficulties are: (1) About half of the 600 or so Cambrian genera are incompletely known or based on poor material, and many have never been placed in any family. In particular the Upper Cambrian forms grade into each other and are hard to separate. Specialist or not, one welters in a morass of names and concepts. (2) Post-Cambrian trilobites seem to fall readily into families and higher groups, but there is a great gap between them and their late Cambrian predecessors. This gap seems to be real, and not merely because many students have worked on either Cambrian or later trilobites, but rarely both. (3) There is a lack of knowledge of the entire, and especially the ventral exoskeleton, and of the ontogeny of representatives of many families.

Attempts were made to base major divisions in trilobite classification on the number of thoracic segments or the size and segmentation of the pygidium. The latter has been used recently by Hupé (1953). Beecher's (1897) classification, using the cephalic sutures, depended on an interpretation that accepted Haeckel's theory of recapitulation. I know of no example in trilobites of ontogeny recapitulating phylogeny, i.e., I know of no ontogenetic stage that resembles a geologically older adult. The use of part of a single morphological character as a basis for an ordinal classification seems unwise (cf. Stubblefield 1936, p. 432, etc.) and in this case has been shown to be unworkable.

It is to be hoped that this classification will no longer be used or taught in the classroom.

In 1936 Stubblefield suggested that many proparian trilobites might be permanently neotenous forms. Størmer (1942) took up this suggestion vigorously, and considered that three orders of trilobites (modifications of those of Beecher) were derived from the supposedly primitive olenellids by arrested development (a partial neoteny) of the anterior cephalic segments. In addition to rejecting Beecher's orders, I consider that certain of Størmer's premises are possibly erroneous, and his classification is no more usable than Beecher's. Hupé (1950) has claimed that partial neoteny is general in trilobites. His evidence is drawn from the study of representatives of two groups, proparia and opisthoparia, each of which is here regarded as being comprised of genetically unrelated genera. Broad morphological trends of change in the cephalon during the Palaeozoic are revealed, but scarcely seem to me to admit of the conclusions arrived at. We do not yet know a single line of evolution with data on the ontogenies of successive genera, and are in no position to assess the importance of neoteny as a process in trilobite evolution. I suspect that adaptation to particular ecological niches (depth, bottom conditions, food supply, etc.) is a far more important factor in trilobite evolution, but to discern its operation is difficult.

If we can avoid being mesmerized by the importance that has so far been attached to cephalic sutures in classification, a different approach is possible, i.e., to consider all the exoskeletal characters (including ventral, and especially axial characters, as Stubblefield [1936] urged), ontogeny (as Størmer [1942] did), and the distribution of genera in space and time. Henningsmoen (1951) has recently made suggestions along these lines and they appear promising.

The Cambrian superfamilies shown in Figure 1 are those used recently by Hupé (1953). The superfamilies outside the stippled area are agreed upon by most students. The ptychoparioid and allied superfamilies, included within the more heavily stippled area, seem to constitute a major natural group of trilobites, but the subdivisions of this group, adopted for convenience here, are not generally agreed upon (cf. Rasetti, 1951, pp. 198-202). The post-Cambrian superfamilies of Figure 1 are the

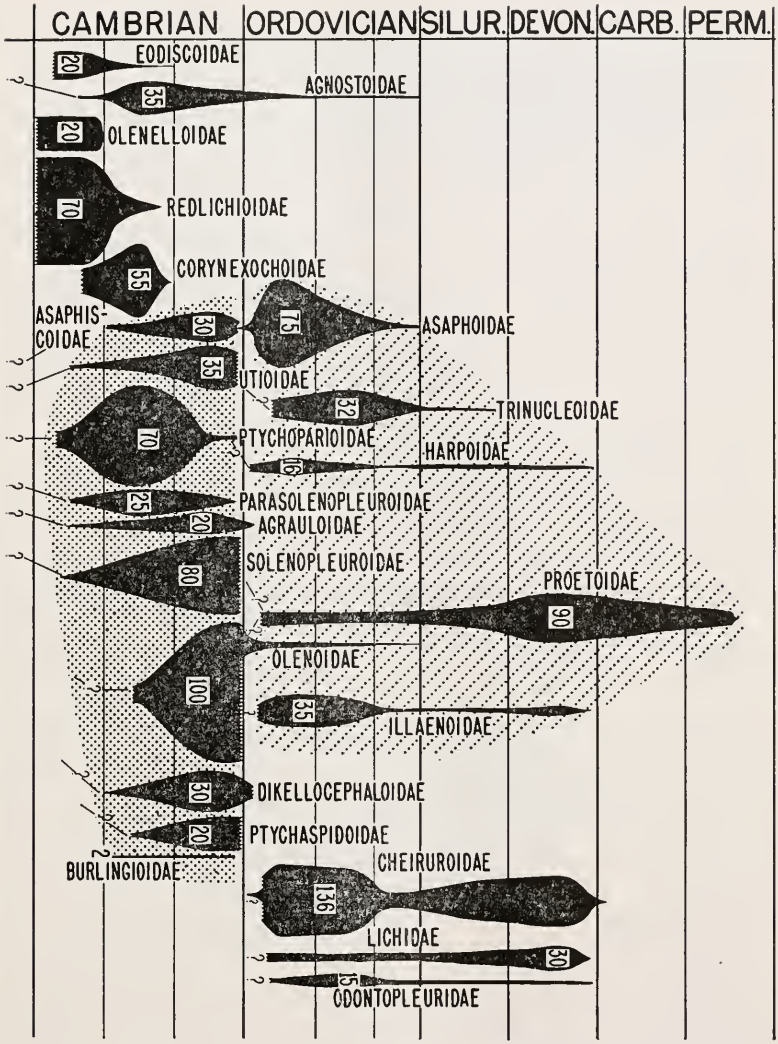

Fig. 1. Range in time of superfamilies of trilobites. Each black area varies in width in proportion to the number of genera recorded at any one time. Total number of genera in each superfamily is given. Data on Cambrian trilobites largely from Hupé (1953). Tremadoc is included in the Ordovician, and Lower, Middle, and Upper divisions of this period and of the Cambrian are indicated. Proportions of length of periods after Newell (1952). Correlations of strata and ranges of genera necessarily generalized. The Ptychoparioidae and allied superfamilies of the Cambrian are included in the more heavily stippled area, and post-Cambrian superfamilies possibly derived from them in the lighter, diagonally stippled area.

groups of families indicated by the shading in Figure 2. In making these superfamilies, besides using axial and ventral characters of adult exoskeletons, W. R. Evitt and I here suggest, as a result of our unpublished studies of protaspids of Ordovician trilobites, that one might group together those families in which early ontogenetic stages have the same general characters, although the adults are distinctly different. This leads, for example, to grouping together as the Cheiruroidae the calymenids, homalonotids, phacopids, encrinurids, cheirurids, and pliomerids. Perhaps more striking is the Asaphoidae, here regarded as including the asaphids and remopleuridids, and possibly nileids, telephinids and cyclopygids. The lichids and odontopleurids — distinctive groups, the origin and relationships of each of which is uncertain — are shown in Figure 1, though they are here regarded as of family, and not superfamily, rank.

The trilobites were marine animals and apparently dominated Cambrian seas. Olenelloids appear first, and are confined to the Lower Cambrian. Other groups occur in the later Lower Cambrian, and some extend only into the Middle Cambrian. These are replaced by the more varied and numerous Upper Cambrian forms, derivatives of the Middle Cambrian Ptychoparioids. "Spindle", "burst", and "truncated burst" patterns, shown by Cooper and Williams (1952) to characterize brachiopod evolution, are equally evident in the trilobites. A lengthy pre-Cambrian history evidently precedes the known history, and the seemingly abrupt appearance of trilobites is apparently owing to their becoming able to form a mineralized exoskeleton. This Cambrian picture is very generalized, owing to difficulties of correlation, and the extinctions may not be as sudden as they appear to be.

There is a marked gap after the end of Cambrian time, only four Cambrian superfamilies ranging into the Ordovician in greatly reduced numbers. Following this great extinction, a number of new superfamilies arise suddenly in the Lower Ordovician, but no new ones arise after this time. Only one Ordovician superfamily, here called the Asaphoidae, is known to arise in the Upper Cambrian. The picture in the Ordovician is one of a last evolutionary burst before new classes, e.g., of Mollusca and Vertebrata, arise to crowd out the trilobites, and the post-Ordo-

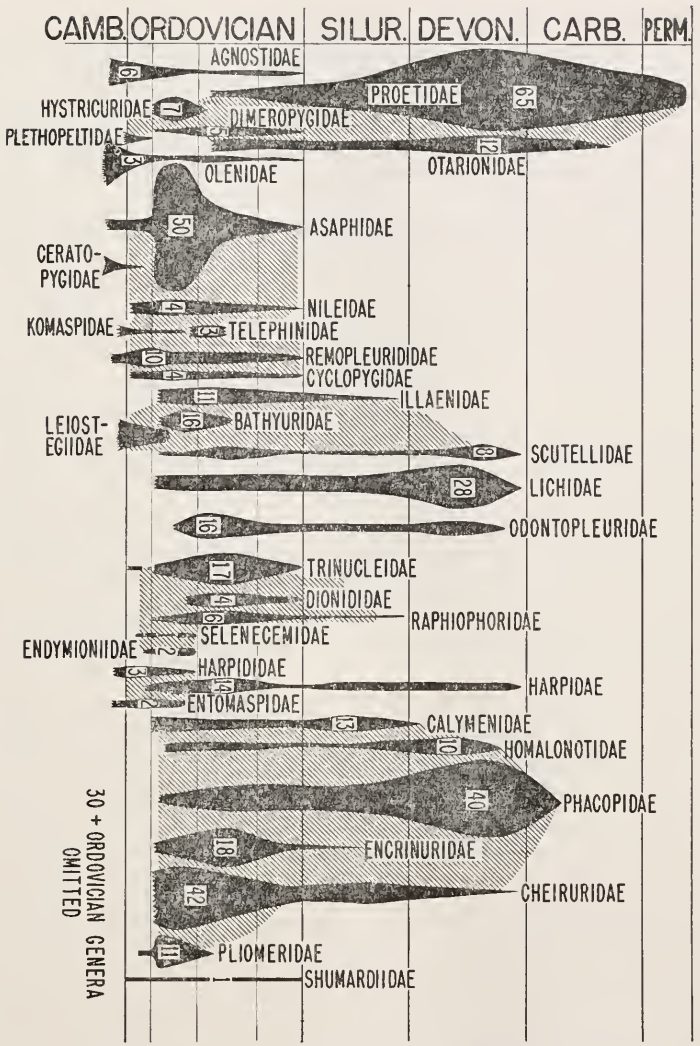

Fig. 2. Range in time of families of post-Cambrian trilobites. Constructed in the same manner as Figure 1. Tremadoc, Lower, Middle and Upper subdivisions of the Ordovician are indicated separately. The shading links those families that have been combined into a superfamily in Figure 1. Leiostegiidae is used in the sense of Whittington, 1953, and Lecanopygidae Lochman, 1953, is not shown.

vician history is one of lingering survival.

Figure 2, composed in the same manner as Figure 1, indicates the range in time of post-Cambrian families. The gap at the base of the Ordovician is more clearly shown, and only in four cases do we know possible Cambrian ancestors of dominantly Ordovician families. Striking is the asaphid "burst", probably occurring simultaneously in unrelated groups in Baltoscandia, America, and Asia. "Bursts" of this type may have taken place in other trilobite families. The great "burst" of new proparian forms begins in early Canadian (i.e. Tremadoc) time and extends into the Champlainian, and we have as yet no notion of the ancestral stocks. Equally puzzling are the Lichidae and Odontopleuridae, arising suddenly, "ready made", apparently unrelated to each other or to other families. The possibility that groups hitherto soft-shelled were acquiring the power to mineralize the exoskeleton cannot be overlooked. The general decline of trilobites from the mid-Ordovician onwards is evident, though inadequate knowledge of Silurian trilobites may falsify the picture. The diversification of certain groups in the Devonian is real, but perhaps over-emphasized as a result of the intensive systematic work of Drs. R. and E. Richter. Undoubtedly, other "bursts" are in part "monographic", and new ones will inevitably be added.

It seems reasonable to suggest that a natural classification should attempt to make orders from groups of related superfamilies. If the superfamilies as shown in Figure 1 are accepted tentatively, the chief stumbling block in the way of the erection of orders is the lack of known connections between the superfamilies. At least four orders might be suggested: one to include eodiscoids and agnostoids, which are perhaps more like each other than either resembles any other trilobite group; a second to include olenelloids and redlichioids; a third for the corynexochoids; and the fourth including the group of ptychoparioids and allied superfamilies included in the heavily stippled area of Figure 1. A lighter, diagonally stippled area includes the post-Cambrian superfamilies which may be derived from ptychoparioids and their allies, and which consequently may be regarded as belonging to the same order. A separate order may be necessary for the cheiruroids, the post-Cambrian proparian trilobites,

the origins of which are at present obscure. Omitted from these groups are lichids, odontopleurids, and various isolated genera and small families of uncertain affinities. It does not seem appropriate to formally propose such orders at the present time, my intention being merely to outline what seems to be a promising line of approach. This approach emphasizes our lack of knowledge in critical areas, and it is this lack which, in my opinion, precludes any satisfactory classification of trilobites at this time.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
VII. *Graptolithina*[1]

By O. M. B. Bulman
Sedgwick Museum, Cambridge, England

Graptolites are extinct colonial organisms, and graptolite phylogeny is expressed in the complicated relations of a succession of colonies. Not only has every individual theca a complete ontogeny (accurately recorded in its growth-lines) but each adult represents a stage in the development of the astogenic unit. Despite the stratigraphical importance of the group, precise knowledge of graptolite phylogeny is disappointingly slight. The general succession of graptolite faunas is, however, well-established, and it reveals a fairly steady process of simplification in the colony and reduction in number of constituent individuals, with phases of elaboration in the skeleton of individual zooids. Only recently have we begun to get sufficiently exact details concerning structure and mode of growth to afford a basis for investigation of the complex problems presented.

These notes are confined to the order Graptoloidea, or true graptolites, but to understand their structure some preliminary reference to the ancestral order Dendroidea is necessary. Here the three types of thecae recognized by Wiman have been shown by Kozlowski to be related to an internal stolon system and probably to have been secreted by only two kinds of individual (plausibly interpreted as male and female). Thus the term "stolotheca" (Wiman's "budding-individual") really designates no more than the proximal, immature portion of the autotheca, since continuity of growth-lines demonstrates that each stolotheca is part of a unit which includes the succeeding autotheca (Fig. 1 *A*, *B*). Consideration of the growth-lines and the stolon system also indicates that there was not (as there is in *Rhabdopleura*, Fig. 1 *E*) a terminal "leading bud" behind which successive individuals are proliferated; but that each

[1] I am grateful to Professor L. Størmer of the University of Oslo for permission to publish this material which is based on a lecture given in Oslo in December 1951.

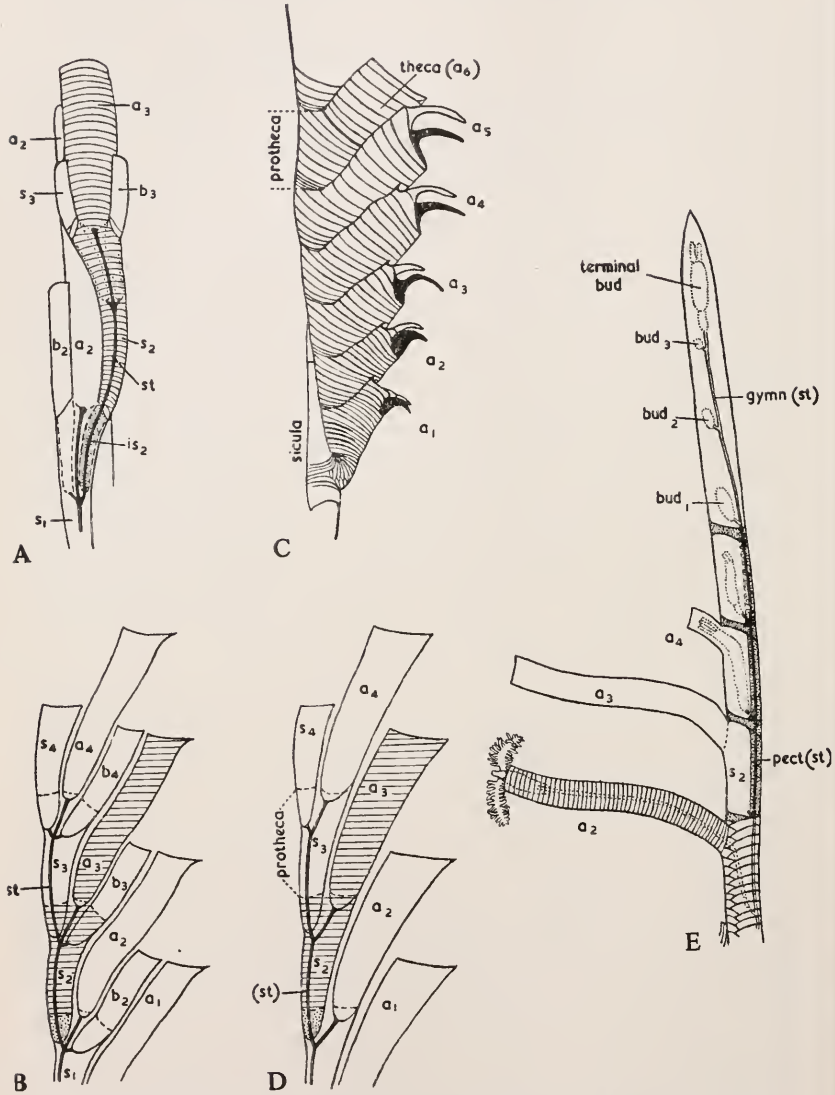


Fig. 1. Comparison of organization and method of budding in a dendroid (*A, B*), a graptoloid (*C, D*) and *Rhabdopleura* (*E*). *a1*, *a2* etc., autothecae; *b2*, *b3* etc., bithecae; *s1*, *s2* etc., stolothecae; *st*, stolon; *gymn.*, gymnocaulus; *pect.*, pectocaulus.

In *A*, *B* and *D*, one complete unit (including stolotheca and protheca) is shaded. Fig. *A* represents the growing end of a branch, and *a3*, *b3* and *s3* are all incompletely developed.

autotheca in turn has represented the terminal bud of its branch, and at a certain stage in its development there are produced from back on its stolon two buds, male bitheca and female autotheca (Fig. 1 *A, B*). The budding processes in *Rhabdopleura,* on the one hand, and the graptolites on the other, exactly parallel the monopodial budding with terminal growing points, and the sympodial budding, described (L. Hyman) in calyptoblastean hydroids.

In the Graptoloidea, branch organisation is considerably simplified by the loss of bithecae (the autothecal zooid, on Kozlowski's interpretation, becoming hermaphrodite), but the stolon

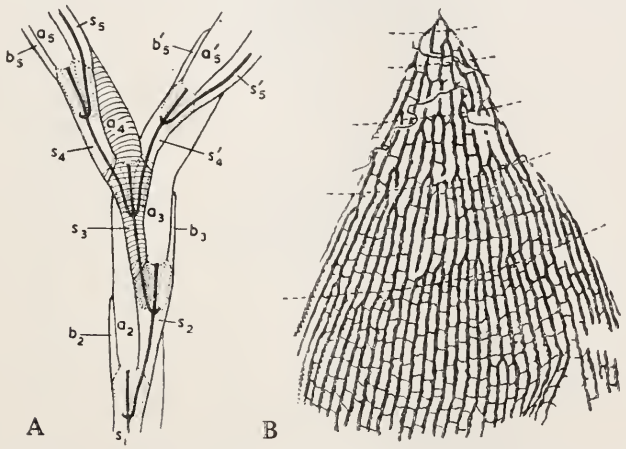


Fig. 2. Mode of branching in a dendroid (*D. flabelliforme*). *A,* branching division with production of two stolothecae (s4 and s'4) in place of stolotheca and bitheca. *B,* approximate zones of branching in the rhabdosome of *D. flabelliforme.* x1.

system may be considered to persist to a limited extent in an unchitinised condition. The occurrence of a small "unconformity" between the growth-lines of adjacent thecae (Fig. 1*C*) even in early stages of colonial development, and the dual construction of each interthecal septum, indicates that each theca buds from the preceding theca as a slightly modified inheritance of the dendroid method of budding (Fig. 1*D*).

Bifurcation in a dendroid branch results from the formation of two stolothecae in place of the normal stolotheca and bitheca

(Fig. 2*A*). Branching is often very regular; more so in *Dictyonema* than in most dendroids and in *D. flabelliforme* than in other species of that genus (Fig. 2*B*). In the Graptoloidea, branching is generally strikingly regular, but since only one type of individual is present in the colony, it clearly results from the formation of two buds in place of one under some periodic stimulus. In relation to the Dendroidea, there is a break here in the evolutionary sequence for which we still lack the material to investigate.

The differences among branched dichograptid colonies are largely due to the spacing and timing of these double buds. There seems to be a general tendency towards reduction in the number of branches in a colony, though few lineages are well established and the recent work of Australian paleontologists suggests that the phyletic relations of the Dichograptidae are much more involved than has generally been recognized. Certainly the two-stiped *Didymograptus* is the successful type, judged by its increasing preponderance in the upward succession; but branch reduction may have taken place either proximally or distally — i.e., *Didymograptus* may be either neotenic or gerontomorphic, if one may use such terms of colonial processes.

Reduction in number of branches implies a reduction in total number of individuals in a colony, which over the whole series may be extreme. A large rhabdosome of *Dictyonema flabelliforme* may have comprised the astonishing total of not less than 35,000 individuals (autothecal and bithecal); a large dichograptid might have 3000 individuals (all of one kind); most leptograptids, dicellograptids and diplograptids have from 100 to 200 individuals (usually nearer the lower limit); while the Silurian *Monograptus* averages about 50 and the late *M. leintwardinensis* consists of only 10 to 17 individuals in a colony.

With the establishment of the simplified autothecal and pauciramous rhabdosome of the typical graptoloid, several structural features make their appearance — some rhabdosomal and some thecal.

Rhabdosomal changes, apart from stipe-reduction, are most conspicuously concerned with orientation relative to the sicula (which itself remains strikingly constant) and the nema suspen-

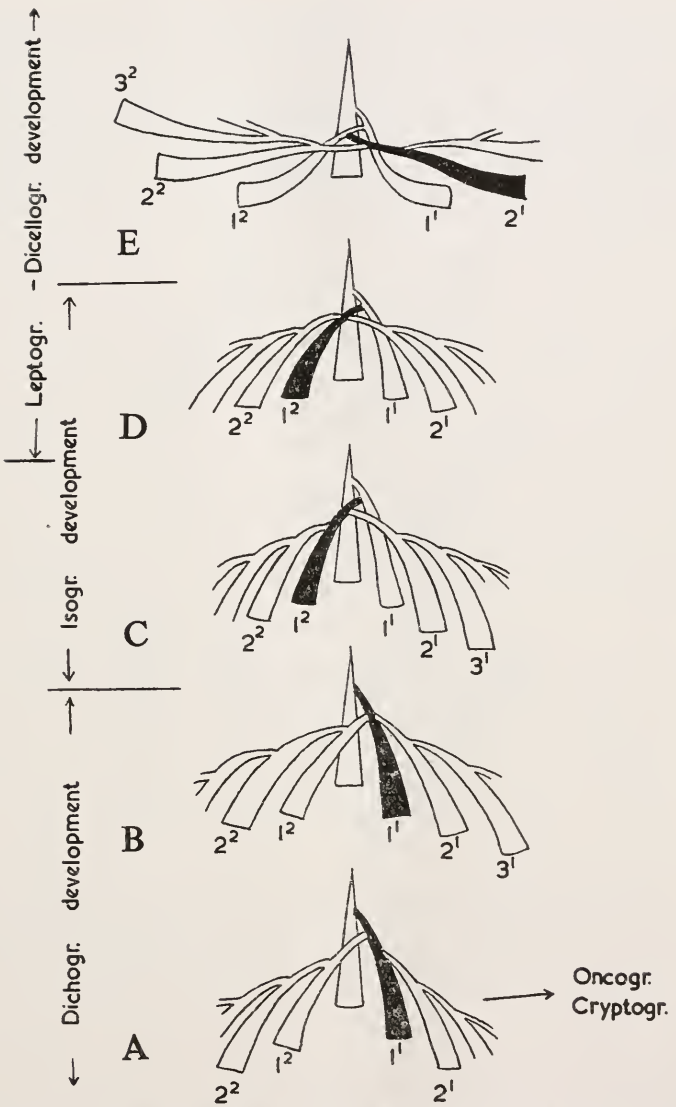


Fig. 3. Progressive changes in the proximal end of the rhabdosome in dichograptids, leptograptids and dicellograptids, showing progressive delay in formation of the "double bud".

sion; the rhabdosome passes from pendent through horizontal to reclined and eventually scandent. This change in direction of growth is an intermittently expressed tendency which affects all graptolites ever since *D. flabelliforme* reversed the normal orientation of a *Dictyonema* rhabdosome to begin the story of graptoloid evolution. It proceeds side by side with a sequence of changes in the development of the proximal end of the rhab-

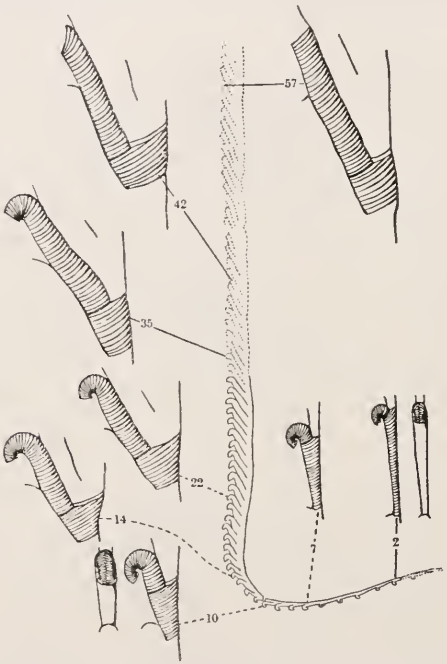


Fig. 4. *Monograptus argenteus* (Nicholson) x2 showing change in thecal character from hooked (proximal end) to straight (distal end); growth-lines on enlargements x10 of selected thecae are partly conjectural, and are inserted to illustrate the form and development of the thecae.

dosome which may be expressed as a progressive delay in the formation of the two buds from which any bilateral rhabdosome develops (didymograptid, leptograptid, dicellograptid or diplograptid). A temporarily stable condition is reached when the first four thecae of the rhabdosome alternate in origin and there are three crossing canals (as is very usual in dicellograptids and

diplograptids), the two buds being carried on th2[1] (Fig. 3). Further evolution to aseptate and uniserial rhabdosomes is mentioned later.

Thecal changes include many types of elaboration and what may be termed "thecal differentiation." The simplest expression of the latter is a distal increase in size, the thecae remaining constant in shape. Even the Dichograptidae show such a distal increase, which contrasts with the uniformity in size of dendroid thecae throughout a rhabdosome. In its extreme expression, it is coupled with thecal elaboration, and successive thecae may undergo progressive change in size and form, as in the many bi-form monograptids (Fig. 4). The available evidence suggests that new types spread gradually along the rhabdosome with time. The linear propagation of buds in one of the simplified Graptoloidea makes such changes more regular than comparable changes in, for example, a compound coral; and it has been compared with the introduction of new characters in a metamerically segmented animal. Less commonly does a new character seem to operate throughout the life of a colony at its first appearance; and occasionally the distal thecae of a rhabdosome may show new features which did not originate proximally, though such features seem rarely conspicuous.

In seeking to attach significance to these thecal changes, it may be added that so far as we are aware, they reflect no difference in habitat; all graptolites are believed to be epiplanktonic, and the remains of many different types occur side-by-side in the rocks. As regards their transmission, it may be noted that whatever modifications the first and subsequent thecae may show, the sicula (the first individual of the colony) remains throughout the Order almost as constant in form as it is in orientation. Every subsequent zooid is produced by asexual budding, the colony being subject to a common genetic control.

In stipe-reduction, change in direction of growth (from pendent to scandent) and the various thecal changes (especially among monograptids), the graptolites furnish numerous instances of "programme evolution", for parallel changes undoubtedly occur independently in many different lines of descent, though few detailed phylogenies have as yet been established by which this assertion can be illustrated.

There seem to have been three major events in the geological history of the Graptoloidea:

I. Derivation of the Graptoloidea from the Dendroidea in late Tremadocian times.

II. Origin of the biserial scandent rhabdosome early in the Ordovician.

III. Origin of the uniserial scandent rhabdosome slightly but appreciably above the base of the Silurian.

I. *Derivation of the Graptoloidea.* This involves loss of dissepiments and bithecae, and was preceded by a change in mode of life, the benthonic rooted habit giving place to a nema-attachment to floating weeds. Such a change had in fact occurred in *Dictyonema flabelliforme* and that varied collection of its immediate descendants the Anisograptidae. Of these, the best known are *Clonograptus* (Fig. 5 *A*, *B*) and *Bryograptus* (Fig. 5 *C*, *D*), but *Anisograptus* (Fig. 5 *F*), *Adelograptus* (Fig. 5 *E*) and *Staurograptus* (Fig. 5 *H*) are also important. They vary in attitude of branches from pendent to reclined, and in number of *primary* stipes from two to four; but all are united in the possession of a nema attachment along with typical dendroid branch structure, and they differ from *Dictyonema flabelliforme* chiefly in loss of dissepiments.

The change from anisograptids to true dichograptids requires the loss of bithecae and is usually accompanied by some reduction in number of branches. Stipe-reduction may come first — *Anisograptus* itself in one of its varieties has only four branches and leads to the triradiate, unbranched *Triograptus* (Fig. 5 *G*) while apparently retaining the dendroid branch structure. Or bithecae may be lost while the number of branches shows little change and may even increase — for there is much to suggest that the Ordovician *Clonograptus* and *Bryograptus* species have a simplified graptoloid branch while retaining the rhabdosome form of their Tremadoc ancestors. The transition from dendroids to graptoloids is clearly a gradual one (in contrast to the other two episodes) and the Graptoloidea may well be polyphyletic, though all seem ultimately traceable (through various anisograptids) to *Dictyonema flabelliforme*.

By the middle of the Lower Ordovician the dominant graptoloid type had become the two-stiped, horizontal or reclined didymograptid. Then progressive delay in the origin of the two buds from which the two separate stipes develop (Fig. 3) leads to the proximal end characteristic of most leptograptids and all dicellograptids of the Middle Ordovician, wherein the first four thecae of the rhabdosome alternate and there are three crossing-canals. Further, these leptograptids and dicellograptids show the substitution of a new type of theca — the sigmoid leptograp-

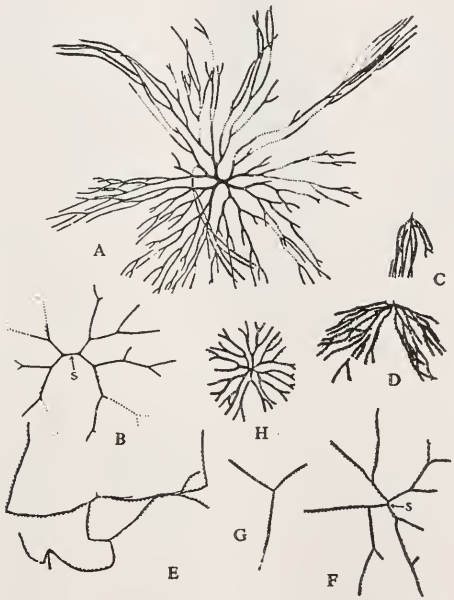


Fig. 5. Representative members of the family *Anisograptidae*. *A, B, Clonograptus* (*flexilis* and *tenellus*); *C, D, Bryograptus* (*kjerulfi* and *patens*); *E, Adelograptus* (*hunnebergensis*); *F, Anisograptus* (*matanensis*); *G, Triograptus* (*canadensis*); *H, Staurograptus* (*dichotomus*). x½ approx.

tid type — for the simple straight dichograptid type. In *Dicellograptus* and *Dicranograptus* this may become further modified in a distinctive manner, the distal end becoming isolated and introverted (Fig. 6 *B, C*).

With the development of the leptograptids, branched colonies

reappear (*Pleurograptus, Nemagraptus* and *Amphigraptus*). No satisfactory explanation of this has yet been given. Since the details of branch formation are still unknown, parallel descent from multiramous dichograptid ancestors cannot be altogether excluded, nor even some kind of "pseudobranching" analogous to the monograptid cladia; but an atavistic interpretation is the one most usually accepted.

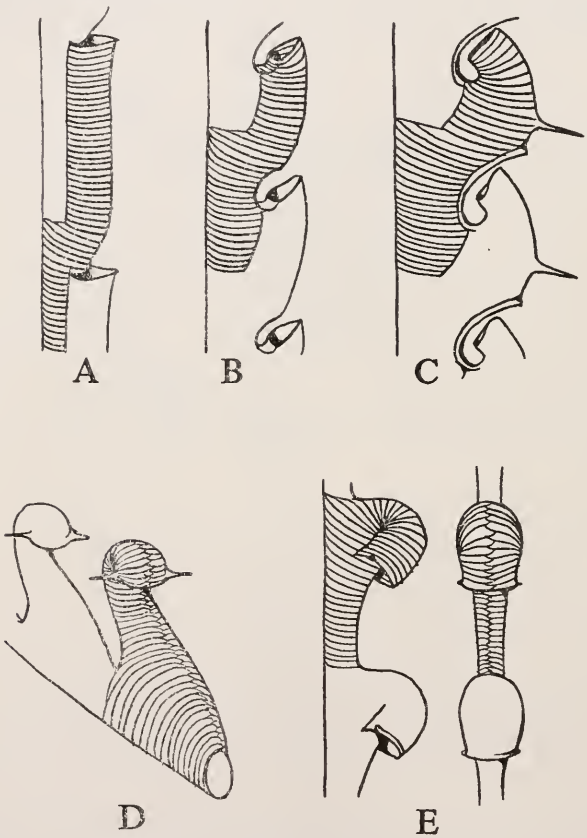


Fig. 6. Selected types of graptoloid thecae. *A*, leptograptid; *B*, dicellograptid (simple); *C*, dicellograptid and dicranograptid (more complex); *D, E*, extreme types of monograptid (triangulate and lobate). Growth-lines, mainly conjectural, inserted for greater clarity.

II. *Origin of the biserial scandent rhabdosome.* The *Dicellograptus — Dicranograptus* series had reached a condition as regards their proximal end (in the alternating origin of the first four thecae) which is practically identical with that of the diplograptids. Moreover, *Dicranograptus* (with its Y-shaped rhabdosome) has long been suggested as an intermediate between *Dicellograptus* and the biserial graptolites. Nevertheless, the diplograptids are the earlier group, and if *Dicranograptus* has any significance in this story it can only be as a contributory factor in a polyphyletic ancestry.

The earliest diplograptid known is *Glyptograptus dentatus* from the Extensus Zone in Britain; by Upper Arenig times it is found in Scandinavia, and by the beginning of the Llanvirn (Bifidus Zone) it had reached Australia and America. Against a background of Lower Ordovician graptolites, its appearance is quite startling; and its structure is so novel that it must surely represent an unusually large but successful mutation. It possesses certain distinctive features in its proximal end which are gradually lost in its descendants (but curiously enough reappear in the only *Dicranograptus* of which we have as yet any detailed knowledge). The significance of these features (the ~-shaped $th1^2$ with its initially upward growth, and the long downward-growing initial part of $th2^1$) is unknown, but somewhat similar features are recognizable in the nearly contemporaneous *Lasiograptus hystrix* and to a less extent in early *Climacograptus scharenbergi.* In fact, the bulk of the true diplograptids may well have a monophyletic origin in *G. dentatus* (using the term diplograptid to include *Diplograptus sensu lato, Climacograptus,* and some as yet undetermined portion of the lasiograptids).

So long as the rhabdosome consisted of two separate uniserial stipes, it was not mechanically possible for the formation of the two buds representing the bases of the two stipes to be much delayed — in fact, the presence of three crossing-canals and the alternating origin of the first four thecae is about as far as this trend can proceed. But there is no such necessary limitation in the scandent biserial rhabdosome, where the septum separating the two stipes may arise at any point along the rhabdosome (Fig. 7 *C, D*). Its earliest appearance is between $th2^1$ and $th2^2$ (Fig. 7*B*) and the septum is then said to be "complete"; but it is

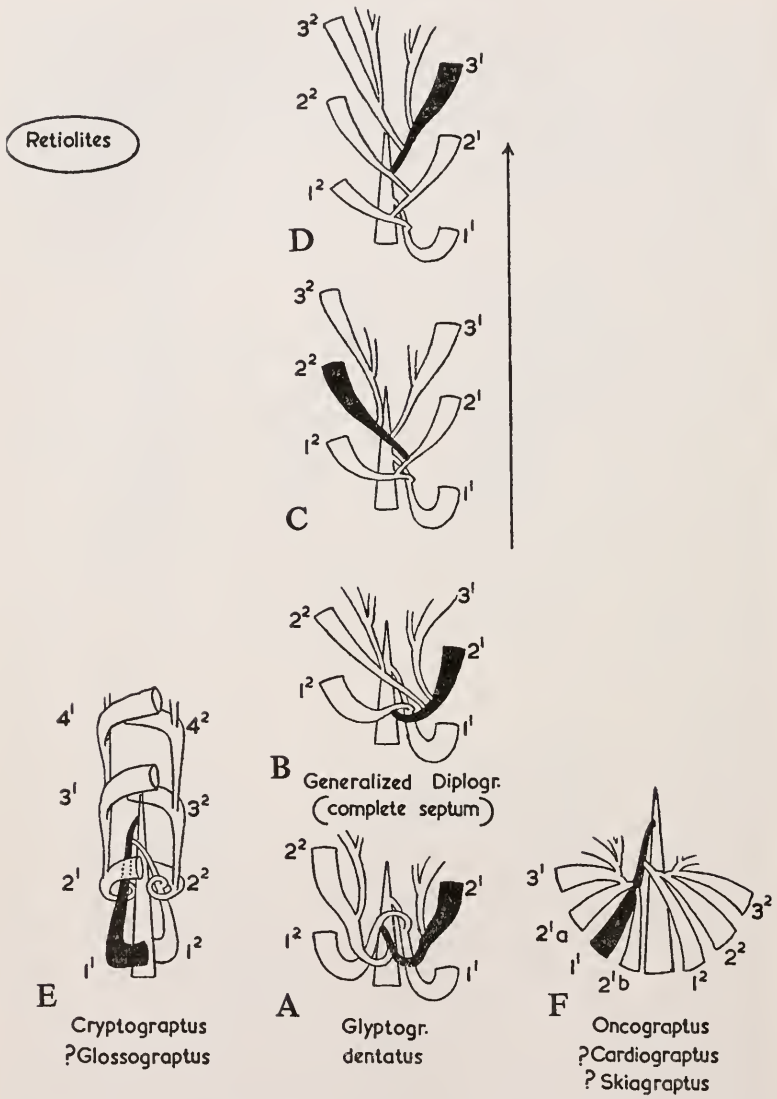


Fig. 7. Progressive changes in the proximal end of biserial scandent graptolites. *A-D*, diplograptids illustrating further delay in production of the "double bud"; *E, F*, proximal end of other scandent biserial graptolites. Precise relations of the thecae in retiolitids remain unknown.

progressively deferred as more and more of the proximal thecae alternate in origin, and may never occur at all if the thecae alternate throughout the rhabdosome.

It may be noted that the thecae in diplograptids, though variously modified, never show the extremes that we encounter among the *Dicellograptus* — *Dicranograptus* series; in particular, no diplograptid so far as I am aware shows any trace of apertural isolation. Thecae remain for the most part fairly generalised and the angularly sigmoidal thecae of *Amplexograptus* and *Climacograptus* represent the most extreme modifications. It is from the more conservative stock (which persists into the Silurian system) that the great wealth of monograptids must be derived.

In addition to the diplograptids proper, there are numerous other scandent biserial forms, such as *Cardiograptus*, *Skiagraptus*, *Cryptograptus*, *Glossograptus*, *Trigonograptus*, *Gymnograptus* and the retiolitids, which are all very imperfectly understood as yet. Many of these appear to have been side lines (some even from the dichograptids) incidental to the main evolutionary story; the retiolitids, however, are probably derived from diplograptids (perhaps more than once), though the chitinous skeleton is so extensively reduced, often to a few structural rods and girders, that it is practically impossible to interpret their proximal end in terms of zooidal succession and development.

III. *Origin of the uniserial scandent rhabdosome.* Failure to produce the pair of buds, or rather, the production of a single bud in place of the pair, cannot by itself convert a diplograptid rhabdosome into *Monograptus*, for even in the simplest and most generalised diplograptid the first four thecae of the rhabdosome are alternating in origin (Fig. 8*A*). This is beautifully illustrated by a form discovered by Dr. Strachan but not yet described, which comprises a uniserial rhabdosome yet possesses th1^2 in its normal diplograptid relation. The change can only effectively come after these *proximal* thecae have substituted a linear serial arrangement for the alternating proximal arrangement of their ancestor, either by reduction or loss of th1^2 and any later "second-order" thecae (Fig. 8*C*), or perhaps more probably by a "merging" of the thecae of the two series (Fig. 8*D*) as postulated by Wiman. Such merging may be combined with the pronounced tendency to an upward direction of growth

which affects the biserial *Petalograptus* and *Cephalograptus*.

Starting from a diplograptid with the most generalised proximal end (a complete septum) it would only be necessary to lose one theca, or to get th1^2 into series between th1^1 and th2^1, for subsequent failure of the "double bud" to result immediately in a monograptid (Fig. 8*C*, *D*). From such an ancestor, there-

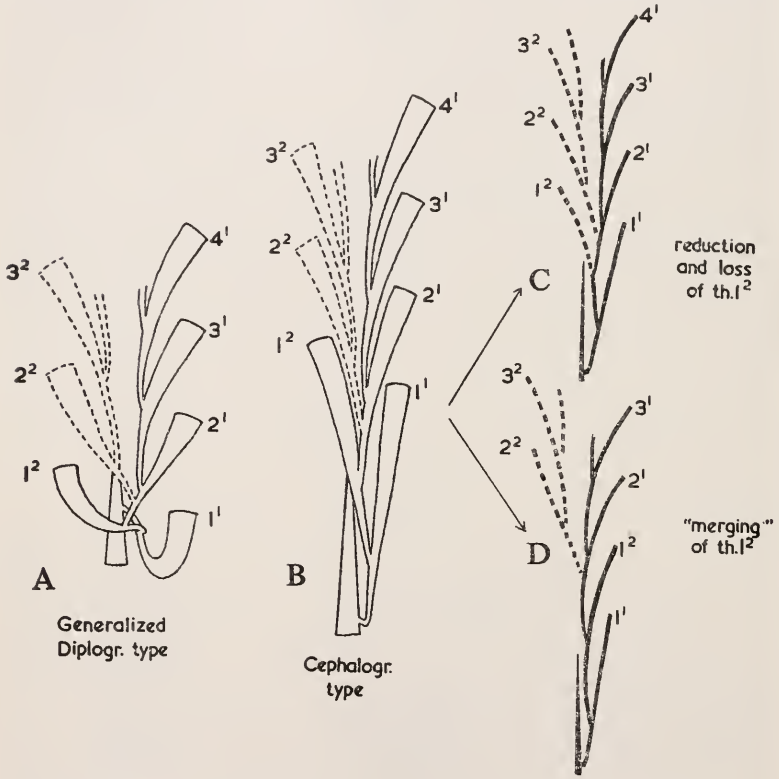


Fig. 8. Diagram illustrating the problem of monograptid origin.

fore, the origin of *Monograptus* is essentially a question of the disposal of th1^2; rearrangement (or loss) of numerous proximal thecae in a form with a delayed septum is more difficult to understand. Yet the well-defined species groups of *Dimorphograptus* suggest that, if this was their origin, the change must have

occurred independently in several lines of descent. It may therefore be thought that *Dimorphograptus* (with a uniserial portion often of considerable length) is less likely to be an intermediate stage than an atavistic form (as Wiman suggested) or a short-lived side line. But it must be admitted that *Dimorphograptus* is essentially pre-monograptid in its range, and its significance in relation to *Diplograptus* and *Monograptus* remains uncertain.

With the origin of the monograptids only a little more than halfway through the evolutionary history of the Graptoloidea, the major phases of structural evolution of the graptolite rhabdosome are passed, and for the next thirty million years the uniserial scandent rhabdosome remains the dominant graptolite form. Thecal elaboration begins anew[1] and may lead to extremes exceeding anything known from the Ordovician. The sequence of thecal elaboration and the structure of "pseudobranched" rhabdosomes of genera like *Cyrtograptus* present many unsolved problems; but the basic form of the colony had in its very simplicity attained a complete stability persisting to the extinction of the Graptoloidea.

[1] In these monograptid elaborations there is an exaggerated development of the *dorsal* margin of the theca leading to extroverted thecal forms, in contrast to the dominant development of the *ventral* lip which produces the introverted Ordovician type of elaboration. Compare Fig. 6 *B,C,* with 6 *D,E.*

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
VIII. *On Development, Evolution, and Terminology of Ammonoid Suture Line*

By O. H. Schindewolf
University of Tübingen, Germany

INTRODUCTION

In comparative anatomy it is a matter of course to use a terminology that is based on the homology of organs. In osteology of vertebrates, for instance, elements of the same origin and development, but often of quite unlike shape receive the same designations. Elements of different origin, however, i.e., merely analogous organs, are sharply distinguished in terminology.

These principles are not yet sufficiently established in the terminology of ammonoid suture line. Here the denominations mostly have been based on the mature sutures, without regard to, or at least without fully utilizing their ontogenetic development. There are, however, several different modes in the development of suture lines, so that it is impossible to base the designations of the lobes merely on their position and shape in the adult suture. This of course would be much simpler, but it would veil the existing differences and thus the natural relations of the forms exhibiting these different suture lines. This method, therefore, is not feasible.

The first authors realizing these failings and initiating a rational terminology of suture line based on its individual development were F. Noetling (1905, 1906) and R. Wedekind (1913 a,b; 1916; 1918). The attempt of Noetling, though ingenious in itself, was a failure, since it involved two wrong suppositions: (1) The foundation, on which the ontogenetic development and phylogenetic evolution of suture line rise, is the primary suture (i.e., the first genuine suture line following the prosuture), but not the prosuture, a larval organ with widely different features. (2) A genetic terminology of suture line cannot be based, as Noetling proposed, on highly differentiated ammonites; it has to

start from the basic structures of the earliest ammonoids, the undifferentiated goniatites.

Wedekind has wisely avoided these two mistakes and has established a terminology unsurpassed until now in consistency and simplicity. I have further elaborated the principles introduced by him, and in this paper I shall discuss in a summary form some general questions concerning the suture line and certain related topics.

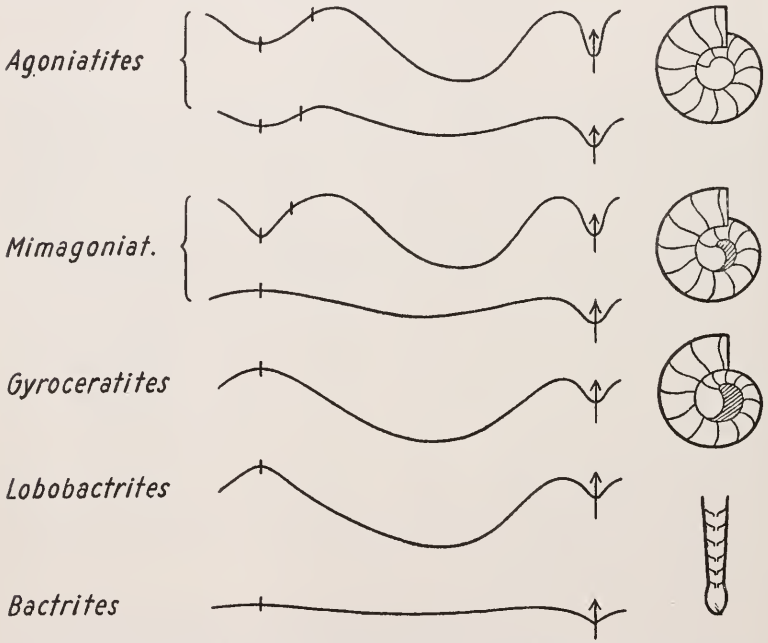


Fig. 1. Suture lines (partly adolescent and adult) and shell shapes of the earliest representatives of goniatites. (Adapted from Schindewolf 1933.)

ACKNOWLEDGMENTS

The writer is deeply indebted to the Geological Society of America for a very generous invitation to attend its 1953 Annual Meeting at Toronto. This gave him the welcome opportunity to deliver this lecture in the symposium of the Paleontological

Society. Dr. B. Kummel very kindly undertook the laborious task of revising the manuscript and of bringing it into the present form. The author wishes to render him sincerest thanks for his trouble and for his stimulating interest.

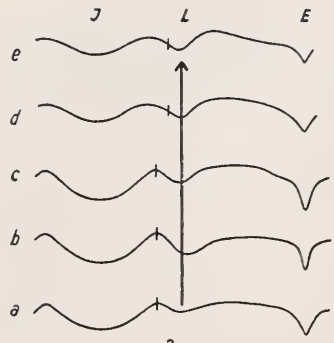
THE EARLIEST GONIATITES

According to my conviction, the ammonoids descend from straight orthocone nautiloids via *Bactrites*, *Lobobactrites*, *Gyroceratites*, and *Mimagoniatites* (Schindewolf 1932, 1933, 1935, 1939a). The Michelinoceratida are an old root stock giving rise to many other groups of nautiloids, to belemnoids and, as it seems to me, also to ammonoids. It may be debated whether *Bactrites* and *Lobobactrites* are to be included in nautiloids or in ammonoids. I prefer to place them in the ammonoids on account of the extreme ventral position of their thin siphuncle and its connection with a ventral lobe, which are important diagnostic features of ammonoids.

Bactrites and *Lobobactrites* (Fig. 1) thus would be the earliest and most primitive representatives of goniatites, still retaining the straight orthocone shell of Michelinoceratidae. The suture line of *Bactrites* is characterized by the possession of a small ventral lobe; otherwise, it is simply straight. In *Lobobactrites* the shell is laterally compressed and on each of the flattened sides a broadly rounded lateral lobe is added, while the dorsum is occupied by a dorsal saddle.

Gyroceratites (Fig. 1), in my opinion a descendant of *Lobobactrites*, has a loosely coiled shell with egg-shaped protoconch and a large umbilical perforation. The dorsal side of the whorls is still without an impressed concave zone. The suture line is the same as in *Lobobactrites*. *Mimagoniatites* (Fig. 1) continues this trend of evolution. In the beginning of its shell it resembles *Gyroceratites*, but soon the whorls begin to cover each other and to develop a concave zone at the dorsal side. The primary suture and the next sutures in the region of the umbilical perforation still retain the dorsal saddle, which in later developmental stages, as soon as the concave zone appears, is replaced by a dorsal or internal lobe. By the inception of this lobe the typical trilobate goniatitic suture line is completed.

The earliest goniatites with tightly coiled shells are *Agoniatites*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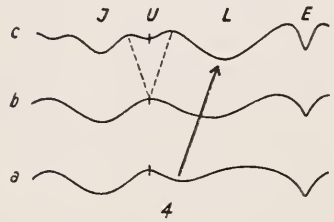
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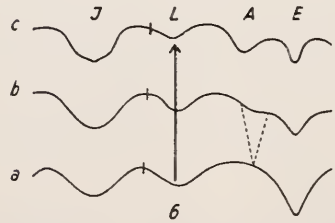
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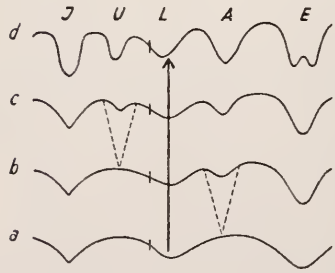
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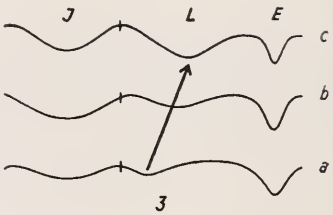
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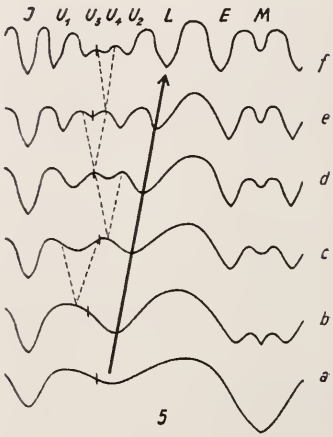
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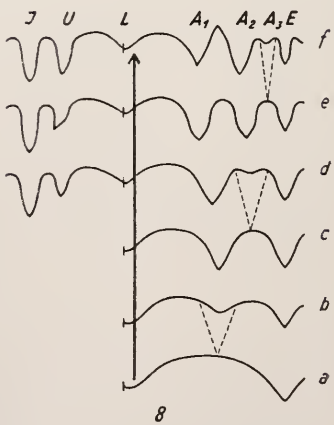
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(Fig. 1) and *Werneroceras* (Fig. 3). In them the protoconch is spirally coiled, the umbilical perforation is lacking, and the whorls from the very beginning possess a concave dorsal zone. As a further progress of evolution the primary suture already is of the type exhibited by the later and adult sutures of *Mimagoniatites:* it is characterized by a dorsal lobe.

It seems to me that this gradual perfection of suture line and of involution is a strong argument in favour of a derivation of the coiled ammonoids from uncoiled orthocone nautiloids. This theory was first advocated by A. Hyatt (1884) and then supported and further elaborated by myself. Having corrected Hyatt's misconception of the protoconch in nautiloids and ammonoids I was able to prove that the small egg-shaped protoconch of michelinoceratids, bactritids, and all ammonoids is the exact homologue of the coarse conical initial chamber of coiled nautiloids.

This statement is incompatible with the view held by L. F. Spath (1933, 1936), that the coiled or typical goniatites evolved

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Fig. 2. Suture lines of *Anarcestes* (*Anarcestes*) *lateseptatus* (Beyr.) from the lower Middle Devonian (*a, b*), *Subanarcestes macrocephalus* Schdwf. from the lower Middle Devonian (*c*), and *Raymondiceras simplex* (Raym.) from the Upper Devonian (*d, e*). (Adapted from Schindewolf 1933 and 1934.)

Fig. 3. Development of suture line of *Werneroceras ruppachense* (Kays.) from the lower Middle Devonian. (Adapted from Schindewolf 1933.)

Fig. 4. Development of suture line of *Foordites platypleura* (Frech) from the lower Middle Devonian. (Adapted from Schindewolf 1933.)

Fig. 5. Phylogenetic evolution of suture line in Manticoceratidæ (and its predecessor *Archoceras*) from the lower Upper Devonian. *a, Archoceras — b, Ponticeras — c, Manticoceras — d, Koenenites — e, Timanites — f, Pharciceras.* (After Wedekind 1913b and Schindewolf 1951.)

Fig. 6. Development of suture line of *Cheiloceras* sp. from the Upper Devonian. (Adapted from Schindewolf 1929.)

Fig. 7. Development of suture line of *Reticuloceras reticulatum* (Phill.) from the Lower Pennsylvanian. (Adapted from Schindewolf 1929.)

Fig. 8. *a-e,* Development of suture line of *Sporadoceras münsteri* (v.B.) from the Upper Devonian. (Partly after Perna 1914.) *f,* Adult suture of *Discoclymenia cucullata* (v.B.) from the Upper Devonian. (After Schindewolf 1951.)

from coiled Silurian and Ordovician nautiloids of the general type of *Barrandeoceras, Tarphyceras* or *Paleonautilus.* The cup-shaped initial chamber, the rapidly expanding first whorls, the mode of involution, the position of the siphuncle and other characters of *Barrandeoceras* and related coiled nautiloids are so profoundly different from those in coiled ammonoids, that such a derivation is impossible. On the other hand, there is in every respect a gradual transition from michelinoceratids through bactritids to the coiled ammonoids. The progressive reduction of the umbilical perforation and the transformation of the protoconch to be observed from Lower Devonian to Middle Devonian species of *Anarcestes* and from them to the Middle Devonian *Werneroceras* definitely postulate such forerunners as *Mimagoniatites* and *Gyroceratites.*

The only difficulty so far was that this evolutionary trend could not exactly be proved by the geological distribution of the respective genera. But since H. K. Erben (1953) recently recorded the occurrence of *Lobobactrites, Gyroceratites,* and *Mimagoniatites* in the Lower Devonian of the Hartz Mountains, these difficulties are eliminated, so that there are no more obstacles to regarding *Lobobactrites* etc. as being the ancestors of the typically coiled goniatites. As a matter of fact the tightly coiled genera *Agoniatites* and *Werneroceras* are geologically younger, and *Anarcestes,* at least, is not known from beds older than those containing *Lobobactrites, Gyroceratites,* and *Mimagoniatites.* The interpretation by Spath, who considered these genera as uncoiled derivatives of *Anarcestes,* is thus no longer tenable.

But these controversies do not affect the question of our suture line. We repeat that all the earlier normally coiled goniatites are characterized by a trilobate suture consisting of the ventral or external lobe (E), the lateral lobe (L), the dorsal or internal lobe (I), and the two saddles E/L and I/L separating them. This elementary suture is the basis from which all the more differentiated sutures of the later ammonoids can be derived. I have termed the three lobes composing this suture the basic lobes or *protolobes,* since they and they alone are common to all the host of goniatites, clymenoids, ceratites, and ammonites. In the later representatives of ammonoids these primary lobes are supplemented by a varying number of additional lobes which may

be called secondary or *metalobes*.

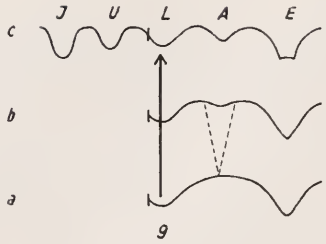
The ventral lobe E and the dorsal lobe I are fixed in the plane of symmetry of the conch; their position is invariable. The lobe E is connected with the ventrally arranged siphuncle; the lobe I is combined with the impressed zone of the whorls.

Variable, however, is the position of the lateral lobe, which has no such limitations. In a few forms (*Gyroceratites, Mimagoniatites, Agoniatites*) it occupies, as a broadly rounded lobe, the middle of the flanks from the very beginning, i.e., from the primary suture. It then shows a position commonly taken as characteristic for the lateral lobe in a stricter morphological sense. In most cases, however, the lateral lobe is situated in the primary suture on or at the umbilical seam. Usually small and shallow, it is separated from the external lobe by a broadly vaulted saddle on the flanks. Then, in later ontogenetic stages this lobe mostly is broadened and shifted to the middle of the flanks (e.g., *Werneroceras,* Fig. 3).

In some few genera (*Anarcestes*, Fig. 2*a, b; Subanarcestes,* Fig. 2*c; Raymondiceras*, Fig. 2*d, e; Archoceras*, Fig. 5*a*), however, it may retain the primary position next to the umbilicus up to the mature suture. Its position thus is not, strictly speaking, lateral. But the gradual shifting of the lateral lobe in related goniatites proves that this lobe at the umbilicus is homologous with the lateral lobe of the adult stages in other genera. It may likewise be termed lateral in the somewhat broader sense that it is the protolobe lying laterally from the plane of bilateral symmetry, indicated by the ventral and dorsal lobe. In any case the characteristic lateral position of this lobe on the flanks is nearly always a secondary one.

THE DIFFERENTIATED GONIATITES

The further elaboration of the suture line consists of the insertion of new lobes. The main process is that of subdividing the saddles. In the apex of a saddle a new lobe appears, shallow in the beginning and then gradually deepening. In the simple trilobate suture of early goniatites and in the likewise trilobate primary suture of the more advanced goniatites two saddles are present: the internal saddle (I/L) and the external saddle (L/E). Each of these saddles may be subdivided and thus give rise to new lobes.



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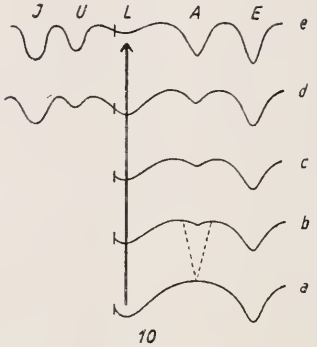

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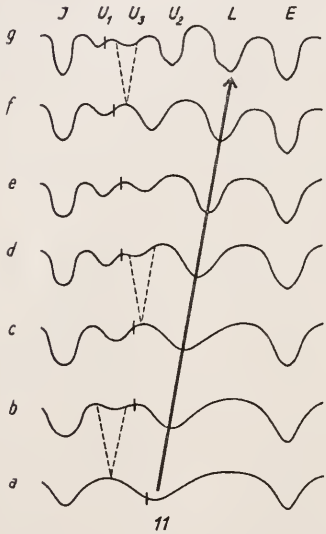

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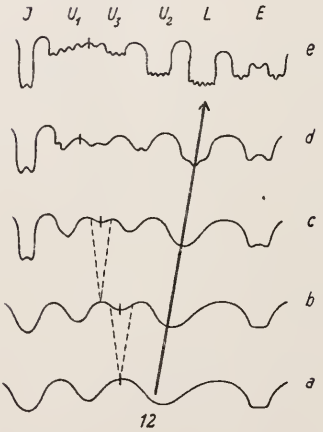

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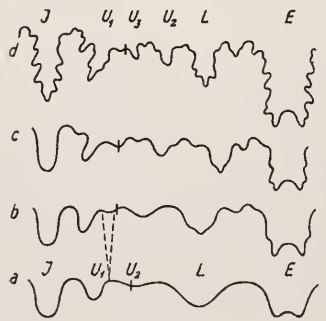

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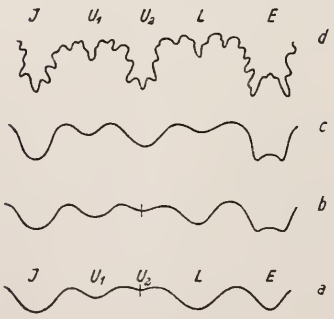

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The lobes which are derived from the internal saddle are termed *umbilical lobes* (abbreviated U), since they are formed in the region of the umbilicus; the lobes originating by the subdivision of the external saddle are called *adventitious lobes* (A). These lobes arise in a very definite order. The umbilical lobes are formed alternately, U_2 follows U_1 at the ventral side, U_3 comes in dorsally to U_2, and so on. The adventitious lobes are inserted in a simple ventrad sequence.

In these differentiated goniatites again the fate of the lateral lobe is different. In the same manner as in most of the early goniatites, it is situated in the primary suture immediately next to the umbilicus and is crossed by the umbilical seam. It retains this position throughout its ontogeny in the case that one or more adventitious lobes are formed. Then the middle of the flanks is occupied by the adventitious lobes. This case is by far the most common among late Paleozoic goniatites. Some examples are shown in Figures 6-10.

On the other hand, if no formation of adventitious lobes takes place, usually a larger number of umbilical lobes arise which displace the lateral lobe from its original position. The second or third umbilical lobe, respectively, is then situated on the umbilical seam and the lateral lobe is shifted to the middle of the flanks or still more outwards. This type of suture line is realized in only a few groups of goniatites, as for instance the Mantico-

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Fig. 9. Development of suture line of *Anthracoceras paucilobus* (Phill.) from the Lower Pennsylvanian. (After Schindewolf 1951.)

Fig. 10. Development of suture line of *Imitoceras* sp. from the Lower Mississippian. (After Schindewolf 1951.)

Fig. 11. Development of suture line of *Merocanites applanatus* (Frech) (and *asiaticus* [Karp.]) from the Mississippian. (Adapted from Karpinsky 1896 and Schindewolf 1929.)

Fig. 12. Development of suture line of *Koninckites* sp. from the Lower Triassic of the Salt Range (Pakistan). Geol. Dept. Tübingen Ce 1043/3.

Fig. 13. Development of suture line of *Strenoceras* (*Strenoceras*) *subfurcatum* (Ziet.) from the Middle Jurassic. (Adapted from Schindewolf 1953.)

Fig. 14. Development of suture line of *Spiroceras bifurcati* (Qu.) from the Middle Jurassic. (After Schindewolf 1951.)

ceratidae (Fig. 5), the Prolobitidae, and the Prolecanitidae (Fig. 11).

The adult sutures of such goniatites, though they originated in two profoundly different ways, may sometimes be very similar in shape and formal composition (Fig. 15). But owing to their different origin the homology of lobes is quite different. What is the lateral lobe in the one suture is an adventitious lobe in the other, and the lateral lobe of the latter suture corresponds to an umbilical lobe of the first one. It is therefore necessary to regard the actual development of suture line in order to determine the true homologies and to gain a proper designation of the

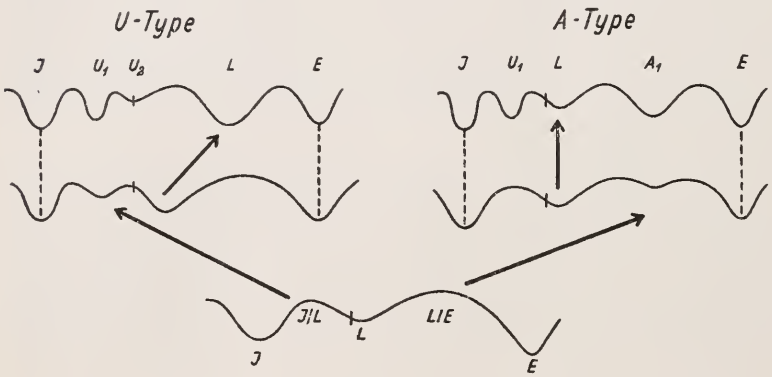

Fig. 15. Diagrammatic confrontation of the U- and A-type of suture development.

lobe elements. This is the more necessary since the two trends of lobe formation are significant for definite groups of goniatites and thus obviously are important for tracing the phylogenetic relations.

For brevity, we will call the type with adventitious lobes the A-type (Fig. 15). Its main characteristics are: One or more adventitious lobes are formed, but only one umbilical lobe is present; the lateral lobe retains the initial umbilical position it held in the primary suture. The other type may be termed the U-type (Fig. 15): A larger number of umbilical lobes, but no adventitious lobes are formed; the lateral lobe is removed outwards from its original position. The U-type is limited to a

small stem of goniatites, while by far the majority of late Paleozoic forms, the Tornoceratidae, Cheiloceratidae, the Goniatitidae with all their derivatives, follow the A-type.

THE MESOZOIC AMMONOIDS

Differing from the Paleozoic goniatites (Fig. 12), the primary suture in Triassic ceratites is quadrilobate, i.e., it contains one element more than that of the former. It is to be interpreted in such a manner, that by accelerated development a first umbilical lobe (U_1) (which in Devonian and Carboniferous goniatites, if at all, was inserted in a much later stage of development) has been added to the three protolobes. The lateral lobe is, from the beginning, situated on the middle of the flanks and afterwards is shifted still more outwards. The primary suture of such a Triassic ceratite (Fig. 12*a*) corresponds thus in every detail to a later developmental stage of e.g. *Merocanites* (Fig. 11*c*).

The further elaboration of the suture line proceeds exactly in the same way by the addition of two other umbilical lobes (U_2 and U_3). In later stages a crinkling of the lobes comes in. The umbilical lobes U_1 and U_3, situated around the umbilical seam, sometimes are strongly enlarged and unevenly differentiated by serration. They may thus simulate a more or less large series of "auxiliary" lobes, which are nothing else than parts of the two umbilical lobes, produced by digitation.

The suture line of the Triassic ceratites follows the U-type, and it can only be derived from goniatitic sutures representing the same type of lobe development, as is the case, for instance, in the Prolecanitidae. Now it is the general conviction, which can be supported by my own studies of Triassic and Permian ammonoids, that the Lower Triassic ceratites are descendants of the Permian Xenodiscidae, which on their part go back to the Carboniferous Prolecanitidae. So our observations and interpretations of suture line lead to the same conclusions as those drawn from other morphological features. They can be used to reinforce and to define more exactly our phylogenetic conceptions.

So far as I can see, all the Triassic ceratites represent the U-type of lobe formation; I have never observed a case of the A-type. It seems to me, therefore, that the A-type prevalent in the Paleozoic was extinguished at the Permian-Triassic boundary and left

no descendants in the Mesozoic (except, at most, some few surviving forms in the Lower Triassic). In the Triassic and, as we will see, also in the Jurassic and Cretaceous the U-type alone is dominant.

The evolutionary cycle of Jurassic and Cretaceous ammonites originates in one of the lineages of Triassic ceratites. So it is to be expected that the same type of lobe formation will be continued by them, and that indeed is the case. The primary suture

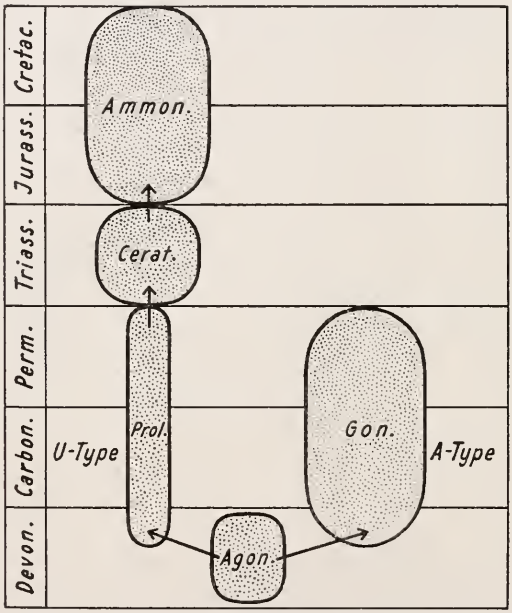

Fig. 16. Diagrammatic representation of the phylogenetic relations of ammonoids.

of these forms (Figs. 13, 14) is quinquelobate; by a further acceleration of development, *two* umbilical lobes are represented in it besides the three protolobes. Their primary suture is thus equivalent to a more advanced stage in the development of the Triassic forerunners. The lateral lobe is situated on the flanks; no adventitious lobes are formed between it and the external lobe.

Summarizing these observations on the suture line we gain a

very simple picture of the broad phylogenetic relationships among ammonoids represented in Figure 16. Of course, this is only a rough scheme, omitting all details, and needing further refinement.

PRIMARY SUTURE AND PROSUTURE

The evolution of the first genuine or primary suture and of its further ontogenetic differentiation shows a definite trend as summed up on the right side of Figure 17. In Devonian ammonoids, the fully coiled goniatites and the clymenoids, the primary suture is trilobate; it consists of the three protolobes I,

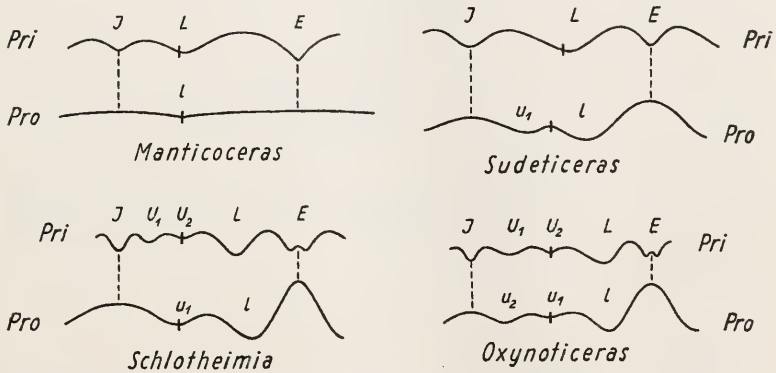

Fig. 17. Comparison of prosutures (*Pro*) and primary sutures (*Pri*) of various ammonoid genera. (Adapted from Schindewolf 1929 and 1942.)

L, and E only. This simple type of suture is retained until the adult stage in early Devonian ammonoids; the lobes only may become deeper. In more advanced Devonian forms one or more metalobes are added during development. The insertion of a first umbilical lobe by subdividing the internal saddle usually takes place between the 20th and the 25th suture.

In Carboniferous goniatites the initial suture is of the same type as that of Devonian forms, but by acceleration of development the umbilical lobe already appears in the next suture or the one immediately following. This quadrilobate stage becomes permanent as the primary suture in Triassic ceratites, and a second umbilical lobe is added in about the 12th to the 16th

suture. Finally, by acceleration, this quinquelobate stage becomes the primary suture of Jurassic and Cretaceous ammonoids. It may be further differentiated by the insertion of a third umbilical lobe in the 12th to the 15th suture line. This is a very impressive example of the acceleration of development, the skipping of old developmental stages and the insertion of new ones into increasingly earlier stages of ontogeny.

The primary suture, however, is not the absolutely first suture line; in the development of every ammonoid it is preceded by another suture belonging to the septum closing the protoconch. It is totally different from the primary suture and has been termed the *prosuture* (Schindewolf 1928, 1929). In its ventral and dorsal parts it is characterized by having saddles instead of the external and internal lobe so highly significant for the normal ammonitic suture. Often the differences between the prosuture and the primary suture are so great that the one in nearly all cases has lobes, whereas the other shows saddles. The primary suture then may look like a reversed prosuture. Furthermore, the number of elements between the ventral and the dorsal side of the two sutures is quite independent. It may be the same (Fig. 17, *Manticoceras, Oxynoticeras*), or it may be larger (Fig. 17, *Schlotheimia*) or even smaller in the primary suture as compared with that in the prosuture (Fig. 17, *Sudeticeras*).

Finally, the phylogenetic evolution of the prosuture from Devonian to Jurassic and Cretaceous ammonoids (Fig. 18, left side) is entirely different from that of the primary suture. It is not necessary to go into the details here, since I have given full descriptions in my earlier papers (Schindewolf 1929, 1942). It may suffice to state that the special character of the prosuture is maintained throughout the whole history of ammonoids, and that the sequence of the newly inserted lobes is quite different from that of the later sutures.

Because of these manifold differences in shape and evolution, it is impossible to deduce the primary suture from the prosuture, whereas the former is closely connected with the following suture lines and forms the basis for their further differentiation. There is a definite break between the two sutures; the morphological features of the prosuture do not find a continuation in the individual development. It is therefore considered as an ephemeral

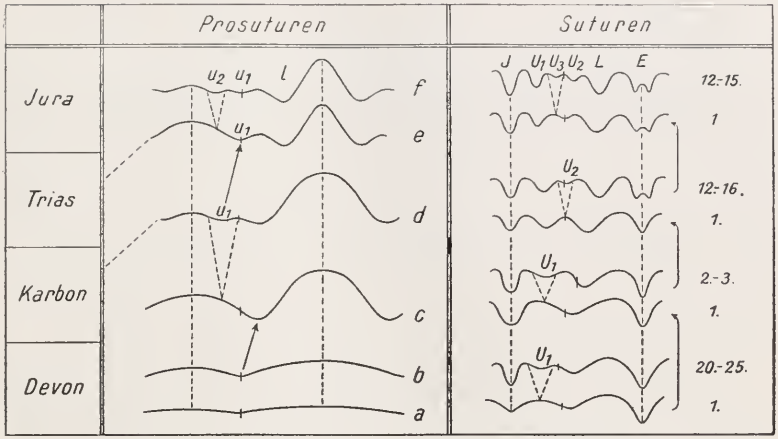

Fig. 18. Phylogenetic evolution of the prosuture and primary suture in ammonoids. (After Schindewolf 1942.)

larval organ and we have to assume that the animal must have undergone a kind of metamorphosis between the secretion of the first and the second individual suture line. Only the latter,

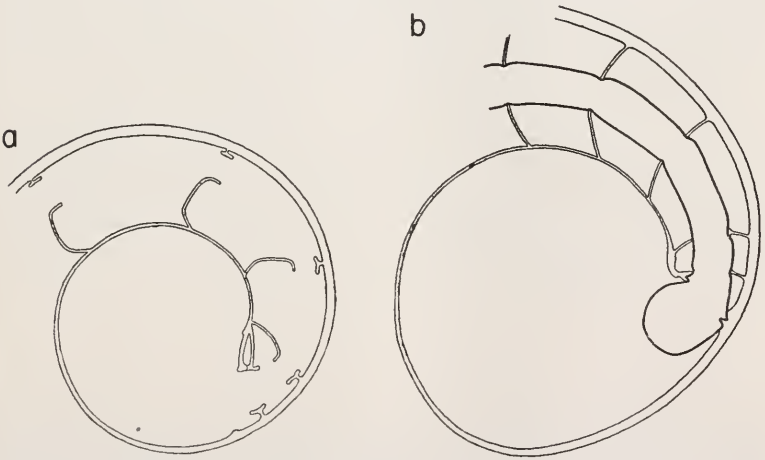

Fig. 19. Median dorsoventral sections through the initial shells of *Goniatites* (*Paragoniatites*) *newsomi* Smith from the Mississippian (*a*), and *Polyptychites* sp. from the Lower Cretaceous (*b*). (After Schindewolf 1939a.)

our primary suture, is a genuine suture line in the usual sense.

A similar difference, like that between the prosuture and the primary suture, is also expressed in the shape of the two respective septa. This may be illustrated by the two median dorsoventral sections in Figures 19*a* and *b*. In *Goniatites newsomi* (Fig. 19*a*) the proseptum delimiting the protoconch differs from the second septum by (1) its greater thickness, (2) its concave instead of convex curvature, and (3) above all by the shape of the ventral part of the septum, which is represented by a minute dent of the shell wall only. The second septum, however, in its ventral part is well developed and bears a hammer-like siphonal funnel of exactly the same nature as in the following septa.

There is thus a distinct break between the first and the second septum, whereas the latter is closely connected morphologically with the following ones. The only difference is the adoral spur at the dorsal side of the siphonal funnel in contrast to the retroflected funnels of the next following septa. It may be due to the lack of room; a backward extension of the siphonal funnel is prevented by the immediate neighbourhood of the proseptum. *Polyptychites* (Fig. 19*b*) from the Lower Cretaceous exhibits a similar profound difference between the first septum and the second septum. Further median sections of goniatites, ceratites, and ammonites, all showing the same phenomena, have been figured by Schindewolf (1939a and 1942).

I cannot agree, therefore, with J. C. A. Böhmers (1936), who assumes *two* prosepta which are said to be different from the remaining septa. It may be that in some cases the second septum shows a somewhat intermediate character between the first and the third. The main break, however, seems to occur from the first to the second septum, thus coinciding with the differences between the prosuture and the primary suture.

PARTITION OF LOBES

Besides the two main trends in the formation of suture line, by subdivision of saddles, there are still several other modes of minor importance. It is not our intention to describe all the different processes forming median saddles, the so-called "sutural" lobes, which could be translated as seam-lobes, or the strange anomalies to be observed in the insertion of umbilical lobes in a

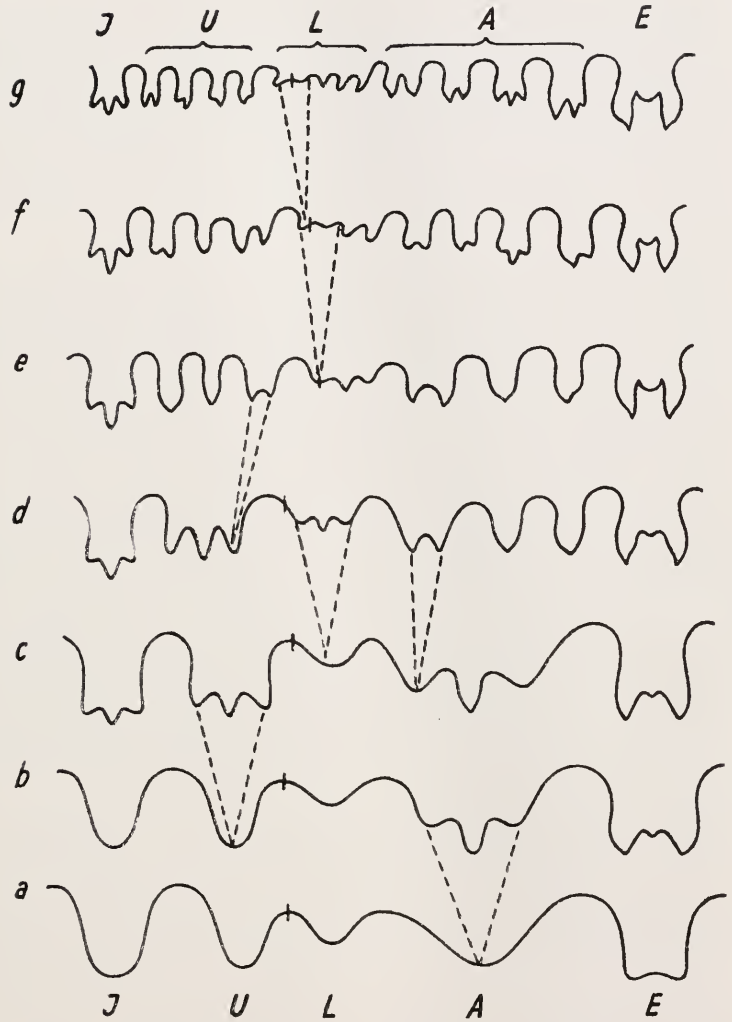

Fig. 20. Development of suture line of *Marathonites dieneri* Smith from the Lower Permian. (Adapted from Schindewolf 1939b.)

certain group of Jurassic ammonoids. But one more process should be mentioned and that is the partition of lobes. It is much rarer than the subdivision of saddles and is subordinate to it insofar as it occurs on the platform of the one or the other of the main types in the elaboration of suture line. Nevertheless, it is very characteristic for several distinct groups of ammonoids, as for instance the Agathiceratidae and Popanoceratidae among the Paleozoic forms, the genera *Metaplacenticeras* and *Coilopoceras* in ammonites.

In these forms one or several lobes are affected by the subdivision. From the base of these lobes two saddles rise and split up the original lobe into three components, which with growing saddles appear as independent lobes. But of course they are not autonomous lobes in the sense of the independent lobes newly inserted by subdivision of saddles. They are only parts of preexisting lobes and are to be marked as such.

This kind of development has been studied in detail by myself in the genus *Marathonites* (Schindewolf 1931, 1939b). Since it and the popanoceratids are on the whole derivatives of the main goniatite group with the A-type of suture line, I assume now that *Marathonites* also will follow this type. The earliest observed stage of development (the primary suture unfortunately is not accessible) then is to be interpreted as noted in Figure 20*a*. Concerning the number and position of lobes it corresponds to the suture lines of *Imitoceras* (Fig. 10), *Reticuloceras* (Fig. 7), *Anthracoceras* (Fig. 9), and other Carboniferous genera. All the lobes are still undivided; only the median saddle in the external lobe makes its first appearance.

In the stage of Figure 20*b* the adventitious lobe A has become trifurcated and shows a development as in the permanent suture of *Proshumardites*. In the following ontogenetic steps (Fig. 20*c-f*) the saddles in the lobe are growing higher and the dorsal element is divided once more into two parts by a saddle rising from its base. So in the suture of Figure 20*g*, the adventitious lobe is represented by a large complex consisting of four apparently independent lobes. In a similar manner the umbilical lobe and a little later also the lateral lobe is split up into a series of components. In the umbilical lobe it is, however, the ventral of the three elements that is bifurcated once more in the same

way as the dorsal one of the adventitious and the lateral lobes.

The adult suture of *Marathonites* and of the other popanoceratids thus contains only five lobes, though it is composed of a large number of elements. It is self-evident that in terminology of lobes this type of development must be distinguished from the mode of subdividing the saddles.

THE SUTURE LINE OF *SPIROCERAS*

In conclusion, I wish to demonstrate a unique, strange case which I recently analyzed and which furthermore may prove the necessity of carefully studying the development of suture line. It concerns the criocone genus *Spiroceras* of the Middle Jurassic. The mature suture line (Fig. 14*d*) is strongly reduced. It seems to contain only three lobes. Besides the ventral and the dorsal lobes there is only one definite lobe which, without knowledge of its development, would be identified with the lateral lobe. Each of the two saddles between these lobes bears in its apex a somewhat deeper indentation. They have been interpreted either as mere crinkles or as reduced lobes, as an adventitious or an umbilical lobe, respectively.

The development of suture line, however, proves that each of these interpretations is absolutely erroneous. The primary suture of *Spiroceras* (Fig. 14*a*) agrees completely with that of the other Jurassic and Cretaceous ammonites (Fig. 13*a*). It is composed of the elements I, U_1, U_2, L, and E. They show the same position and relative size as usual. In the course of development, however, the porportions are profoundly changed. The initially very shallow lobe U_2 quickly becomes deeper and larger, whereas the neighbouring lobes are gradually reduced in size. The large lobe of the adult suture, supposed to be the lateral, is thus in reality the accelerated lobe U_2, while the two insignificant crinkles are to be homologized with the lateral and the first umbilical lobe!

This is a very surprising result, which by no means could have been deduced from the adult suture line. It corroborates our thesis that a scrupulous study of ontogeny is necessary for a consistent interpretation of suture line. Only in this way can the true homologies of lobes be recognized and distinguished from mere analogies. If such investigations could be done in all crucial

cases, the suture line would prove still more valuable for revealing the natural relationship of ammonoids than is the case today.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
IX. *Macroevolution and the Problem of Missing Links*

By Alexander Petrunkevitch
Yale University, New Haven, Conn.

The problem of missing links had its inception in Darwin's theory of evolution. As soon as his *Origin of Species by Means of Natural Selection* was published, it was generally assumed that if this theory is correct then there must be an unbroken chain of connecting links between living animals and their fossil ancestors. Because of the direct bearing of the theory on the question of the origin of man, the search for missing links was taken up by anthropologists, paleontologists and zoologists. It has continued unabated for almost a century and presumably will continue to occupy our attention for many years to come. However, with the universal acquiescence in the idea that all species of plants and animals, man included, are the product of evolution and not of creation, the problem of missing links assumed an aspect different from its original one which concerned the proof of evolution as against special creation. At present evolution is an accepted fact. What remains in dispute is only the method of evolution. On the answer to this question there is considerable disagreement. Opinions differ not only about the ancestry of various categories of animals, but also about the probability of the eventual discovery of now missing connecting links, as well as about the possibility or impossibility of explaining the origin of larger categories by a process of speciation as attempted by Darwin. The reason for such disagreement lies not in insufficiency of evidence, but in the undeniable fact that, with the exception of observations made in breeding experiments, all evidence relating to ancestry is of an indirect nature. As such, it is subject to doubt, error and different interpretation.

The truth of this statement becomes immediately apparent when one considers the question of the relationship between the coelenterates and the flat-worms. Basing their opinion on an analysis of extensive data gradually accumulated during more

than a century of careful research, the majority of zoologists derive the flat-worms from the coelenterates, especially from the ctenophores or comb-jellyfish which they resemble in many respects. The greater complexity of organization of flat-worms is generally explained by progressive evolution and by the formation of new characters better adapted to crawling. On the other hand, the Yugoslavian zoologist Hadži (1953), using the same data, derives the coelenterates from the flat-worms. He explains the origin and the greater simplicity of structure of the former as a result of regressive evolution. According to his theory, rhabdocoele Turbellaria gave up their mode of life as crawling animals, became sessile and gradually lost all structures which were now useless to them. At the same time they acquired a new plan of structure, becoming radially symmetrical out of originally bilateral animals. Developing his theory to its logical end, Hadži reverses the current idea of the evolution of coelenterates also within that group itself. He considers the Anthozoa to be the oldest group which developed first and then produced the Scyphozoa and finally the Hydrozoa. According to his interpretation, the latter represent the acme of regressive evolution. The ctenophores Hadži derives from another class of flatworms, namely the Polyclada.

Hadži's ideas cannot be dismissed lightly. The fact that they are diametrically opposed to the ideas promulgated by other zoologists is not caused by insufficiency of knowledge or by faulty logic. In the absence of direct evidence which could be furnished only by breeding, both his and his opponents' ideas are based entirely on similarities of structure. Such similarities can be arranged in a series of either increasing or diminishing complexity of organization. The controversy could be settled, but even then only partially, by paleontological evidence. If it were possible to show that one of these groups of animals appeared at an earlier geological period, then the later group could not possibly be the ancestral one. But this would be insufficient as proof of the correctness of the opposite contention, namely that the older group produced the younger one. There is another possibility, besides that of direct descent, that can account for the existence of similar structures in groups otherwise differing in many ways. It is the simple assumption that both groups are

descendants of the same ancestral stock, but that their relationship to each other is that of "cousins" and not of parents and children. We are all familiar with such cases when animals originally considered to be direct ancestors were later demoted to the status of more or less distant relatives representing branches of a common ancestral stem. This applies not only to larger and smaller categories of animals, but also to closely related genera as exemplified by the history of the derivation of man from anthropoid apes.

Leaving out of consideration the *direction* of evolution, i.e., the question as to whether in a given case we have to do with progressive or regressive changes, the strength of an argument in favor of direct ancestral relationship grows with the increase of similarities in number and in degree. If speciation is assumed to be the only method of evolution, operating since the appearance of animal life on earth, then it should not be difficult to find connecting links between species possessing the greatest number of similar structures and the greatest degree of similarity. The theory demands that new species be produced by old species and in that way produce new genera; or better, that new species become eventually so different from their parental ancestors that the erection of a new genus for their reception becomes necessary; that some of the new genera produced by speciation require the erection of new families and so on until through the same process of continued speciation new orders, classes and phyla are produced. Let us assume for the sake of simplicity that a new species can be produced through the transformation of a population owing to the gradual spread of a single new mutation — the extinction of the parent species and the survival of the new species being the result of natural selection. With the exception of special cases, the number of deaths corresponds to the size of a population regardless of its composition, decreasing or increasing with the population. On the other hand, the number of fossils is always much smaller than the number of individuals which die, because the majority of the bodies disintegrate before they can become fossilized. Consequently fossils represent only a random sample of a living population. If that population consists of a much greater number of individuals of the parental type with the characters of

the original species than of individuals with modified characters, as one would expect to be the case at the beginning of speciation, then all fossils of that generation may be entirely of the original, parental type, because the ratio between living and fossilized individuals is so great that the chance of mutants becoming fossilized is greatly reduced and approximates zero. But when in the course of time and owing to the survival of the fittest, the mutants have reached the point at which their number in the living populaion is equal to that of the parental type, i.e., when the population consists of 50 per cent of the old type and 50 per cent of the mutant type, then each random sample of the population will also contain the same proportion of both types. Environmental conditions and chances of fertilization being the same for both types, both should be represented by an equal number of fossils. From now on, with an increase of mutants over old types, fossils should also show an increasing number of mutants. The number of fossils of the old type will now grow smaller and smaller until their complete disappearance at an earlier date than the actual extinction of the living species. Thus for the total span of time required for the production of a new species the number of fossils of the parental type should be the same as that of the mutant type. In other words, connecting links between any two species standing in a direct relationship of ancestor and descendant should be as common as the two species themselves. If, as Darwin's theory assumes, all higher categories of classification have been produced by speciation of the kind with which we are now familiar (owing to the extensive work of geneticists), then the ratio of connecting links between all higher categories should also be the same as between species all the way back to the first appearance of fossils in the strata of the earth, forming an unbroken chain between them. There should be no missing links at all except in cases of animals whose fossilization is either impossible on account of the softness of their body, causing its rapid decay, or is indeed so rare for the same reason, that if such fossils were ever found it would be impossible to decide whether they represent the typical or the mutant type.

The above analysis is correct only on the assumption that speciation is a continuous process. That mutation is a constant

process is generally accepted today. Thus Dobzhansky (1951) says on page 73, "The mutation process constantly and unremittingly generates new hereditary variants — gene mutations and chromosomal changes." But if it could be shown that in each line of evolution there are long periods of rest between periods of speciation, intervals during which newly produced species continue their existence as such and no new mutations or heritable changes of any kind are produced, then, of course, the ratio between typical and mutant fossils would be considerably greater. It would depend on and reflect the duration of each pause. But the greater ratio would apply only to the *total* number of fossils during the combined periods of pause and speciation. The ratio for the latter alone would still remain the same, only the horizon containing the fossils of both types would be reduced to a thinner layer corresponding to the time between the beginning of speciation and the extinction of the parental species. In cases of common species there should be no difficulty in finding connecting links.

The existence of such pauses was assumed by de Vries, the creator of the mutation theory (1901). In his address before the society of German naturalists and physicians he considered the average duration of each interval between the periods of mutation to be no less than 4000 years. Accepting the then current idea that the age of life on earth amounted to 24,000,000 years, de Vries arrived at the conclusion that 6000 mutations sufficed to complete the evolution of now living phanerogams from their unicellular ancestors to the present state of their organization. (de Vries, 1901, p. 63). Although the total time allotted to the existence of life on earth has been greatly increased since de Vries's time, owing to new methods of measurement devised by students of radioactivity, its span seems still to be much too small to account for the evolution of all animals by the slow process of speciation. Species are not produced suddenly, by a single mutation. Even with the selection intensity equal to 0.5, it requires 30 generations to bring a mutation frequency to 100 per cent (Lerner, 1950). The time required for the production of a new species varies considerably. But with the exception of special cases, speciation is much slower. Haldane, in his controversy with Lunn (1935, p. 164), admits that "selection is the only agency

which can lead to important changes within times measured in millions of generations." Simpson (1944, p. 69), in discussing the classical case of the evolution of the horse, writes: "In larger populations dominated by selection, a million years may not suffice to introduce a new species and relatively seldom suffices for evolution of generic rank. Note the previous estimate that the actively and progressively evolving tertiary horses took on an average 8,000,000 years for evolution from one genus to the next." If we put the average time for the production of a vertebrate species at only 500,000 years, and regard the process of evolution as being continuous, it would have to be completed from fish to man within only about 625 steps from one species to another. If we accept intervals between speciation equal to the time required for speciation, we would have to accept that only 312 species-transformations separate man from fish.

But the slow tempo of speciation is not the only reason for my belief that the evolution of the higher categories of animals could not have been accomplished by speciation. If it depended entirely on speciation, then *formation* of new species either by production of new characters or by modification or loss of old species characters would be insufficient for achieving the evolution of higher categories. To do this, every animal of whatever phylum, class, order or family would have to be first completely dedifferentiated to the state of organization of the ancestor of the corresponding category. Production of new characters required for the establishment of a new phylum by speciation is a step toward complication of organization, not toward its simplification. Nobody could maintain that our ancestors were more complexly built than we are. To be sure, we are familiar with numerous cases of regressive evolution leading to secondary simplification of structure, due to various causes, such as parasitism, loss of locomotion with adaptation to sessile existence, etc., but such dedifferentiation is not identical with that which is prerequisite for the evolution of a new phylum or class. A creature like the parasitic cirripede *Sacculina* or the parasitic copepod *Lernaea* (the adult females of which have no resemblance whatsoever to other, free living species of Crustacea because in the course of development their organization becomes reduced to nothing but reproductive glands and nutritive tubes), would still

have to return to the state not of their own nauplius which cannot reproduce, but to that of their ancestor which still could not only reproduce and develop into an adult of its own species, but which was so primitive that it still possessed the potential ability of developing into a new order of Entomostraca. If that ancestor of Entomostraca were to engage in the evolution of a phylum other than that of Arthropoda, to which it belongs, then it would have to dedifferentiate further yet to the state of the ancestor which still possessed the potential ability to start the evolution of any other phylum, including even the vertebrates. The necessity of dedifferentiation of this kind before a species can resume creative speciation in a new line may be called the *law of precession*. It involves the formation of a chain of regressive links in addition to that of progressive links. Of course, nobody imagines that a Recent primate, carnivore or monotreme could ever start evolving a new phylum, because all Recent mammals are so complex that one could not expect fundamental changes in their anatomical structure, but attempts are still made to derive vertebrates from various groups of invertebrates, arthropods from annelids, and practically all classes of arthropods from trilobites. If phylogeny through speciation were possible, then the law of precession would have to be taken into account, the time required for the evolution of the animal kingdom would have to be extended to include the time required for dedifferentiation. There should be a chain of transitional links similar to that of progressive evolution, but reversed in the order of sequence and representing the steps of regressive evolution, preceding and prerequisite for each start on a new line of progressive evolution.

It is well known that not only species, but genera and even families present transitional characters, while orders, classes and phyla are sharply delimited. There are no transitions between scorpions and spiders, between beetles and butterflies, between fairy-shrimps and daphnids; there is none between Crustacea, Arachnida and Hexapoda; between Arthropoda and Echinodermata and so on. Some striking resemblances exist, but they are only external resemblances. Some cockroaches *look* like beetles, but are in every other way typical cockroaches. A Carboniferous arachnid of the order Ricinulei resembles some beetles to such

an extent that its discoverer Buckland actually mistook it for a beetle and gave it the generic name *Curculioides, Curculio* being a well known genus of beetles. But *Curculioides* was soon proven to have all the characteristic structures of an arachnid, which could not possibly be confused with the characteristic structures of beetles. Nor can resemblances between so-called homologous structures be regarded as evidence of close relationship and used as examples of connecting links. This lamentable overestimation of their value is still broadly in vogue. Invertebrate zoologists and paleontologists cling tenaciously to the old concept of homology as defined by Owen. In the case of arthropods they regard as sufficient evidence of homology the presence of even widely dissimilar appendages on the same segment of the body, counted in an early embryonic stage from its anterior end backward. Vertebrate anatomists, beginning with Owen himself, did not use this method because of the fluctuation in the number of cervical vertebrae in birds, but never doubted the homology of such structures as the foreleg on a mammal and the wing of a bird. The segmentation of the arthropod head is still a subject of controversy. While we may safely homologize the segmentation of an insect leg with that of an arachnid leg, although they may not belong to the same body segment, we may not do this so easily when comparing the arachnid chelicerae with the crustacean second antennae even though they are regarded as belonging to the same cephalic segment. The fact is that under the influence of experimental zoology the concepts of homology and analogy have undergone considerable change and the very distinction between them is now not simple to define. This is further complicated by the phenomena of so-called homomorphism (Novikoff, 1953), the existence of similar organs in unrelated classes of animals, and by cases of accidental and experimental development of eyes and of appendages on segments of the body to which they do not normally belong. All this and similar facts make the use of "homologous" organs as an argument in favor of direct ancestry or even of close relationship, not nearly as convincing as it was thought to be some time ago. They are suggestive of some relationship, but by no means a proof of it. We have to admit and to face the fact that such connecting links representing gradual transition from one phylum to another, from one class

to another and from one order to another do not exist in invertebrates. Vertebrate anatomists seek to prove that such transitions exist between the classes of vertebrates. They derive the higher classes of vertebrates from fishes on the basis of structural evidence. But even if such transitions among vertebrates can be demonstrated, there may be some other explanation for their existence than that offered by evolution through speciation — an explanation which would bring them in line with the invertebrates.

It seems clear that if we are to solve the problem of evolution within the available geological time, we must either admit the possibility of a much greater speed of speciation or restrict the scope of speciation and accept the existence of another mode of evolution in the case of the higher categories. The speed of selection is undoubtedly correlated with the speed of reproduction. Other factors are known which also have a bearing on the speed of speciation. But the paleontological evidence is rather in favor of slow speciation, while the evolution of higher categories often shows a remarkably higher speed. Moreover, evolution by speciation offers no other answer for the lack of connecting links between higher categories, except the lame one of the extreme rarity of such fossils. On the other hand, an answer involving the assumption of another mode of evolution was given several times, although its bearing on the problem of missing links seems to have been overlooked. Goldschmidt (1933, 1940) called this mode macroevolution; Lunn (1935) spoke of it as major evolution; Simpson (1944) referred to it as megaevolution. In view of the objections raised by geneticists, zoologists and paleontologists to the existence of another mode of evolution differing from that of speciation, we must first consider wherein phylogeny differs from ontogeny besides the already mentioned lack of connecting links, and then show why macroevolution gives an answer to the above questions.

When one considers the development of any animal, one is forced to regard the regularity of the process as something much more striking than its casual and slight irregularities, as if the development followed a predetermined design. The sequence of the stages of development is fixed, some following one upon the other, some beginning at the same time and either running

synchronously to completion or if asynchronously, yet at a predetermined rate and time required for completion. If ever a deviation of the development from its prescribed course takes place, it is either corrected by the intervention of regulatory forces or else leads to the formation of monstrosities or even causes the death of the embryo. In closely related species outward differences in development appear only toward maturity, even though microscopic study and breeding reveal differences in the egg. The less two animals are related to each other, the earlier some differences in their embryonic development appear. In species belonging to different families, differences may appear shortly after the appearance of the first rudiments of organs; in different orders — even shortly after gastrulation. It is now known that all such changes are the result of corresponding, invisible changes in the genes either through mutation, recombination or loss. This knowledge is relatively recent and did not exist in the past century. When Ernst Haeckel (1866) proposed his Biogenetic Law according to which ontogeny is an abbreviated recapitulation of phylogeny, he conceived it on the evidence of the regularity of development and of striking similarities between early embryos of distantly related species, as had been pointed out even earlier by von Baer. Haeckel (1877) further elaborated his theory by postulating the existence of a hypothetical ancestor of all metazoa. He imagined that it was a free-living, marine animal having the simple structure of a gastrula and proposed for it the name *Gastraea*. Haeckel's theory attracted a number of enthusiastic supporters, but was later attacked from all sides and almost discarded as a fanciful speculation. Some of Haeckel's examples were indeed fanciful and the objections to them are valid and remain in force. Other objections require careful reexamination. It was pointed out, for example, that the development of Recent animals takes place along narrow lines which are similar in only closely related groups, but differ widely in the case of different phyla; that free-living animals morphologically similar to the later embryonic stages do not exist; that the gastrula stage can be easily explained as a result of special mechanical and physiological requirements of growth and nourishment; that free-living larvae with the structure of a gastrula, such as the pluteus, bipinnaria, auricularia, tornaria, trocho-

shaera, veliger, etc., are as highly specialized as the corresponding adults and therefore cannot be used as evidence of relationship or, as Yves Delage (1898, p. 331) puts it in discussing the origin of Prochordata, that they represent at best a very distant relationship of the Prochordata to the Echinodermata, as if the latter were separated from the ancestors of the former considerably before these acquired their distinctive characteristics.

After serious examination of the value of these objections on the basis of evidence adduced by others and that assembled by myself in the course of long study of arthropods and especially of arachnids, I have come to the conclusion that most of the objections are wrong because of a literal interpretation of Haeckel's Biogenetic Law which, when properly interpreted in the light of modern knowledge, is perfectly sound and universal in its application. The objection that no living or fossil animal has the structure of the hypothetical gastraea endowed with the ability of self-perpetuation is quite correct as far as it goes, but it is also true that if it ever existed in the past, a fossilized gastraea, on account of its small size and perishable constitution would be not only much rarer than even a fossilized medusa, but also would be much more difficult to find, unless preserved in something like the Old Red Sandstone of Rhynie Chert and handled in a similar way, i.e., in thin sections through the rock, and studied with the aid of a microscope under high power. It is quite true that free-living larvae having the structure of a gastrula are all specifically distinct and that the invagination of the blastoderm, leading to the formation of a gastrula can be explained as a response to physico-chemical stimuli, but such an explanation does not take into account the genetic composition of the hereditary apparatus of the nuclei. The fact that pressure on the elastic wall of a thin rubber balloon may produce an invagination similar to that produced by gastrulation does not prove that pressure is the only requirement in both cases. All attempts to explain even such a simple phenomenon as locomotion on the basis of simple physical laws have broken down completely unless the voluntary element is taken into account. The free-living larvae of Echinodermata, Annelida, Mollusca, etc., are indeed specifically distinct, showing modifications of both the adaptive and the passive type, but their possession of

specific characters does not change the fact that they all have the same basic structure of a gastrula. The objection that there never have been any free-living animals comparable to the later embryonic stages is not only true in this respect, but far from being a refutation is, on the contrary, a direct confirmation of the Biogenetic Law, because it is quite true that beyond the gastrula stage the development of any animal species repeats the development of its ancestors and is thus a recapitulation of its own line of descent. A species of *Drosophila* does not repeat in its ontogenetic development the evolution of a starfish or an octopus. It repeats only its own evolution. It follows the development of an arthropod through the stage of a gastrula to the point at which that arthropod ancestor became an insect, then the development of that insect ancestor to the point when it became a fly and finally the development of the fly ancestor through the stage of the *Drosophila* ancestor to the stage of the particular species under observation. Anything else is impossible and unthinkable, because it would contradict every principle of genetics. A deviation from this rule is possible only when some change in the genetic composition has taken place or some subsequent injury has interfered with normal development.

The objection of geneticists to a mode of evolution different from that of speciation (based on the assumption that changes of the magnitude of macroevolutionary ones would be so rare and so disadvantageous that they would be eliminated by selection or would be lethal from the start), is as unsupported by evidence as the assertion that if they were viable we would meet with such changes either in nature or in the laboratory. Both objections are based on observations of living animals, apply only to speciation, and are gratuitous when applied to macroevolution which took place in past geological eras. Highly disadvantageous non-heritable monstrosities of various kinds do not necessarily cause premature death, nor prevent monsters from giving birth to normal children. The celebrated Siamese twins, Cheng and Eng, married two sisters in America, had 22 children by them and died in 1874 at the ripe age of 62 years, one a few hours after the other, because they could not be separated from each other surgically. Human monsters with two heads, two chests and four arms, but a single pelvis and a single

pair of legs have been observed several times. One of the most celebrated cases of this type came to the notice of King James IV of Scotland, who took the twin monsters under his protection and gave them an education. They lived 22 years (Martin, 1880). Monsters among invertebrates are not uncommon. One finds them in medusae, in worms, in starfishes, in molluscs, in arthropods. Many of them become sexually mature and reproduce. Under my own observation a female *Cynthia* moth with rudimentary wings copulated with a normal male and laid a normal batch of fertilized eggs. I have caught, in Saxony, a male beetle *Prionus coriarius* copulating with a normal female. The male had deformed elytra and lacked one leg. In Panama I watched a male spider *Nephila clavipes* copulating with a normal female. He lacked three of his legs and was of small size, while in the same web were several normal males of larger size. If one wished to list all monsters which lived to mature age one could write a whole book about them. But "hopeful monsters" of macroevolution, a humorous term proposed by Goldschmidt to emphasize their ability to survive, are not even real monsters. They differ from non-heritable monsters in that the changes which produce them involve only fundamental structural characters, which are not necessarily a handicap and may have been even of advantage. These changes also differ from those produced in speciation by their magnitude and suddenness. Moreover they are restrictive in eliminating other changes of a similar nature in their own line of evolution and are therefore directive as pointed out by various writers. And in addition, evidence of their existence and of their independence from speciation is abundant, as may be seen in arachnids, at least in so far as the formation of suborders and families is concerned. I have discussed the evolution of Arachnida in former contributions to our knowledge of their geological past, and of the principles which should govern the natural classification of that class. Here I want only to point out by the example of scorpions the difference between macroevolutionary and microevolutionary changes, and the fact that both are plainly preserved in fossil material. The macroevolutionary change on which I based the classification of Carboniferous scorpions involves the loss of thoracic sternites and the shifting into the place vacated by

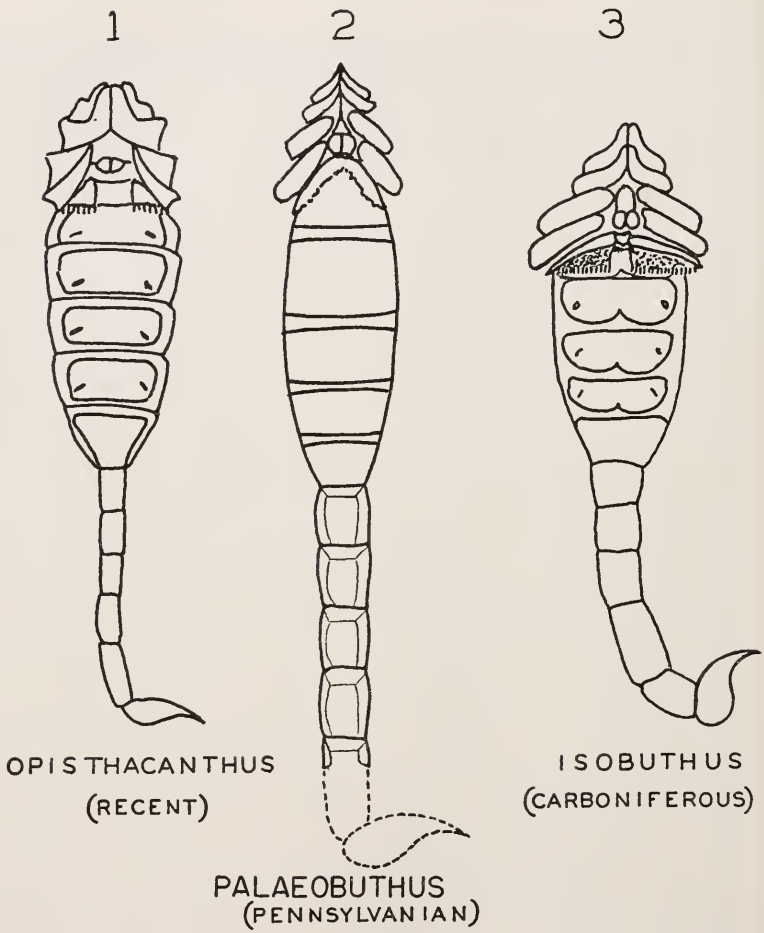

Fig. 1. The ventral surface of *Opisthacanthus elatus* (Gervais), a Recent scorpion of the family Scorpionidae. The arrangement of its coxae is the same as in the fossil family Eoscorpionidae.

Fig. 2. The ventral surface of *Palaeobuthus distinctus* Petrunkevitch, a Pennsylvanian scorpion of the family Isobuthidae. The arrangement of its coxæ is the same as in *Isobuthus*, but the posterior edge of its abdominal sternites is straight as in *Opisthacanthus*.

Fig. 3. The ventral surface of *Isobuthus kralupensis* (Th. and L.), a Carboniferous scorpion of the family Isobuthidae.

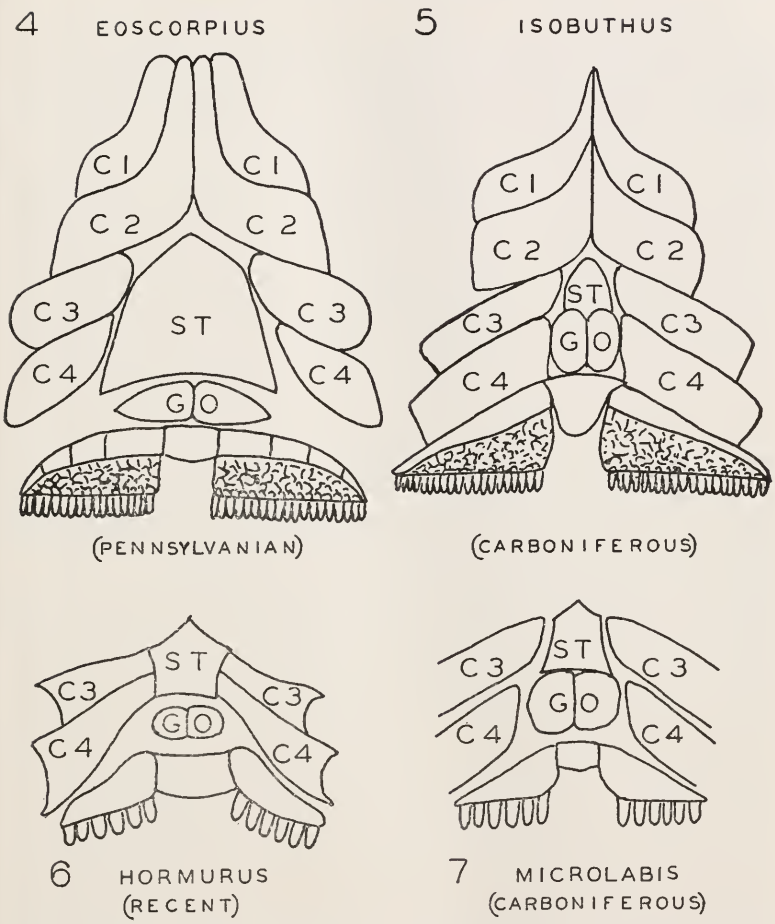

Fig. 4. The sterno-coxal region of *Eoscorpius typicus* Petrunkevitch, a Pennsylvanian scorpion of the family Eoscorpionidae. Notice that the arrangement of its coxae is the same as in the Recent *Hormurus*, while the structure of the combs resembles that of *Isobuthus*.

Fig. 5. *Isobuthus rakovnicensis* Fritsch, a Carboniferous scorpion of the family Isobuthidae. Notice that its disposition of coxae is the same as that of *Microlabis*, but its combs resemble those of *Eoscorpius*.

Fig. 6. The sterno-coxal region of *Hormurus australasiae* Fabricius, a Recent scorpion of the family Scorpionidae. Notice that the disposition of its coxæ is the same as in *Eoscorpius*, while its combs resemble those of *Microlabis*.

Fig. 7. *Microlabis sternbergii* (Corda), a Carboniferous scorpion of the family Isobuthidae. Notice that the disposition of its coxae is the same as that of *Isobuthus*, while its combs resemble those of *Hormurus*. Abbreviations: C_1, C_2, C_3, C_4, coxa of leg 1, 2, 3 and 4; *GO*, genital opercula; *ST*, sternum.

them of the second and third abdominal embryonic sternites represented in the adult by the genital opercula and the median piece of the combs. This change (Figs. 1-7) is possible in several different combinations, all of which are represented in the fossil material, but only two of which are shown in the figures and only one of which survived and produced all Recent scorpions (Figs. 1, 4, 6). This is not the extreme modification. Yet all extinct modifications, even that of the original type in which only the first sternite was lost, survived long enough to produce other changes by speciation, namely the change in the shape of the posterior edge of the abdominal sternites (Figs. 1-3), and the change in the size and shape of the combs and in the number of their teeth (Figs. 4-7). The straight posterior edge of abdominal sternites is the original type found in all Recent scorpions without exception and in almost all fossil scorpions. It is also found in the genus *Palaeobuthus* of the Family Isobuthidae to which the other two genera, *Isobuthus* and *Microlabis,* also belong. *Isobuthus* has bilobed sternites. In *Microlabis* the first and second sternites have a small median indentation, while the third sternite is clearly, though not deeply, bilobed. It seems to be an "ornamental" change rather than anything else. The combs are sense organs of unknown function, but being sense organs, they probably represent "adaptive" speciation. *Eoscorpius* is a genus of the fossil family Eoscorpionidae from which all Recent families may be derived. *Hormurus* is a genus of the Recent family Scorpionidae. Figures 4 to 7 show similar, parallel changes in two different families, changes consisting in a reduction of the number of teeth, and therefore independent of the macroevolutionary changes which gave rise to different families.

In this connection I would like to point out that the chief difference between macroevolutionary and microevolutionary changes is not the magnitude of the change, but the nature of the trend which produced it and the fact that no dedifferentiation is required in the case of macroevolutionary changes. The magnitude in itself is a very relative concept. All evolutionary changes are of the saltatory, discontinuous type, even those which appear to be gradual. Moreover, a change in the genetic composition of chromosomes may produce an outwardly invisible change of considerable importance, such as color blindness for

example, but it is a saltatory change, nevertheless. When a series of small changes confronts us, we speak of them as gradual or transitional. When a change is considerable enough to make the difference glaring, we look for the missing connecting links, not realizing that the change in itself is the connecting link between the parents with the original structure of their body and the offspring with the modified structure. This connection can be discovered only through a study of fundamental trends. Macroevolution leaves no evidence of its operation other than accomplished changes, nor any regressive links, for it is not subject to the law of precession. But it offers an indirect evidence of its existence by leaving unaffected all specific characters in the branches of the same line, characters subject to independent speciation.

Oparin (1953) has shown how self-perpetuating, living substance of the nature of colloidal protein may have originated on earth. He has also explained how the original substance may have broken up into individual "droplets" and how these droplets may have formed clusters by coacervation. He also pointed out how such clusters may have become cellularized and thus given rise to primitive animals. Being a biochemist, Oparin left the problem of further evolution to zoologists and botanists. Whether or not his outline of the origin of life is correct in every detail, his approach to its solution is sound and we may accept his hypothesis as far as the formation of clusters. Finding further support in Haeckel's Biogenetic Law and in the principle of macroevolution, we may now attempt to get some insight into the phylogenetic evolution of animals. To begin with, instead of deriving the Metazoa from this or that class of Protozoa, as is usually done in phylogenetic trees, we may assume that individual "droplets" developed a somewhat different genetic apparatus, remained single and produced the kingdom of *Protista,* while clusters cellularized and some of them became the ancestors of the kingdom of plants, others changed into free-living *moreae* with a structure resembling that of a morula and became the ancestors of the kingdom of *Metazoa.* The next change must have resulted in the transformation of the morea first into a blastea and then into a gastraea, retaining the ability of asexual self-perpetuation, presumably by transverse division comparable

to strobilization in the scyphostoma larva of the medusae. Such a gastraea must have had the shape of an ellipsoid, a ciliated ectoderm, a nutritive endoderm and a mouth at one end of its longitudinal axis. As it still possessed the potentiality of eventually developing into any of the future phyla, this stage may be properly called *protogastraea*. Its plan of symmetry must have been radial and its asexual reproduction made it still "immortal" in Weismann's sense of this word as he applied it to the Protozoa. Now some molecular change in the genetic apparatus must have brought about a differentiation of the cells into reproductive ones and somatic ones, restricting the "immortality", or as I prefer to call it "the ability of self-perpetuation" to the reproductive cells, while the soma became the protective carrier of the reproductive cells, and the perishable residual of the organism. Before this change, competition between individual protogastraeae was strictly intra-specific because there did not exist as yet any other species of Metazoa. But now, owing to the separation of the soma from the reproductive cells, a new type of competition arose. Under the influence of this competition the protogastraeae were changed into *Metagastraeae* with potentialities now restricted to the production of individual phyla. This macroevolutionary change which produced as many species of metagastraea as the number of future phyla, did not need to be synchronous in all cases. It may have occurred repeatedly as long as protogastraeae survived. But the complexity of the structure of animals found in the Cambrian makes it certain that the separation into phyla had been completed before that era. The difference between the various species of metagastraea at that time may have been only intracellular, in the structure of the genetic apparatus; the outwardly visible specific differences were probably developed by speciation at a later period. It would be futile to speculate further as to how the present modes of reproduction involving complicated life cycles were evolved, because we have not enough evidence to do so. Such evidence could be assembled only by extensive study of comparative embryology and anatomy. For the present we may abide by the assumption of an independent origin of all phyla from specifically different metagastraeae, but all produced by the same type of protogastraeae. But even resigning myself to this limitation, I

believe that the thoughts which I have presented here in brief outline give us a much simpler picture of evolution, and are in closer agreement with the fossil evidence and with the available span of time that has passed since the first appearance of animal life than does the theory of evolution by speciation.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
X. *Evolution of Late Paleozoic Invertebrates in Response to Major Oscillations of Shallow Seas.*

By Raymond C. Moore
University of Kansas, Lawrence, Kansas

INTRODUCTION

The Problem

Among the many factors which influence evolution of invertebrate organisms, particularly those of benthonic habitat in a marine environment, are composite effects of broad oscillatory movements of shallow seas.

When such seas transgress widely over portions of the continental shelf, areas available for occupancy by marine organisms may be expanded vastly. During the enlargement of shallow seas and for a time after maximum expansion has been attained, competition for food and for a place of attachment is made easier. Concurrently, the opening of new territory for habitation by bottom-dwelling organisms may foster and then tend to stabilize adaptive changes. This should operate in roughly the same manner as alteration of human societies which has marked the spread of white men throughout the North American continent.

Regression of a shallow sea introduces conditions opposite to those of transgression. Inevitably it shrinks space (*Lebensraum*) available to the shallow-water marine organisms. It causes crowding, and increases competition to survive. If retreat of the shallow sea is measured in terms of many hundreds or thousands of square miles, not only must populations be drastically reduced but the effects on those that continue to live may be profound. Weaker, less well adapted marine invertebrates are sure to be weeded out and only animals which can hold their own, perhaps expanding at the expense of those which disappear, belong to the remnant shallow-water fauna. It seems reasonable to construe times of marine regression as more significant in terms of accelerated evolution than times of marine transgression.

Inadequacy of Evidence from Living Faunas

For the most part a zoologist working on living marine organisms can only theorize about effects on life of the enlargement or reduction in area occupied by a given shallow sea. He cannot make surveys of bottom-dwelling populations in some chosen area in a manner serving to demonstrate change introduced by expansion or contraction of the selected seaway. Quantitatively significant advance or retreat of seas is much too slow to permit observation of its effects on bottom dwellers in any one region. Collection of reliable data would require millennia. Accordingly, the neo-zoologist can only compare assemblages of organisms in broad continental-shelf areas with those occurring in narrow shallow-sea belts, trying to interpret the origin of such differences as he finds. Although some of the differences may reflect evolution at work, he cannot safely identify them, let alone evaluate them.

Paleontological Investigation

A paleontologist is able to study the record of life in three dimensions, for he can both observe areal distribution of organic assemblages represented by remains preserved in rock strata, and he can study the nature of closely adjacent different assemblages higher or lower in the geologic column. The nature of this advantage is very well known.

In most sections of conformable marine strata, fossils collected from two or more contiguous layers are properly inferred to represent samples of successive populations in an area continuously occupied by the sea. Whether the collections are derived from a former biocoenose or give evidence of a thanatocoenose, for present purposes makes little difference. The small fraction of the paleontological record reveals at most the nature of slowly changing conditions that reflect lapse of geologic time (excluding effects of possible physical changes in environment). Study of fossil collections from such conformable strata does not supply information on effects of advancing or retreating seas.

If the faunal assemblage in one layer is known to represent part of an extremely wide-spread shallow-sea deposit, whereas a not-far-distant higher or lower assemblage represents a similar

fraction of organisms living in a much restricted seaway, this would begin to meet the conditions of the problem proposed for investigation. Unfortunately, it is almost impossible to find geological conditions which can be so interpreted reliably.

Evidence from Cyclic Deposits

Another approach is the comparison of successive widely distributed marine faunas, each of which is independent, representing a shallow-sea transgression wholly distinct from others. Such independence may be demonstrated by the presence of a disconformity, indicating nondeposition and possibly erosion of previously formed deposits, which intervenes between the compared fossiliferous marine strata. It may be proved also by widespread occurrence of nonmarine deposits belonging to a time of considerable marine regression, where these subaerially formed beds are found between two sets of shallow-sea deposits. Late Paleozoic sedimentary rocks of the northern midcontinent region in the United States offer ideal examples of such cyclic sedimentation. They include many units consisting of very widely distributed marine strata that record extensive inundation of the continental platform, and they include equally widespread nonmarine deposits that occur between the marine units. The beds which were laid down on land incontrovertibly prove absence of the sea at the time and place where they were formed. If fossil invertebrates found in one of these independent widespread marine deposits are lineal descendants of similar organisms found in a next-lower broadly distributed marine band, then the differences between them, if any, should measure the effects of sea retreat and re-advance between the times of extensive marine sedimentation.

The examination of successive assemblages of marine fossils belonging to cyclic deposits in Kansas is comparable to study of a series of individual pictures ("frames") in a motion picture film. Each such picture furnishes a single glimpse of an ever-moving subject separated from the slightly different next picture, by blank film. The blanks (nonmarine record) of the stratigraphic succession are much longer than those of ordinary film, however.

The cyclic aspects of Pennsylvanian strata and to a lesser

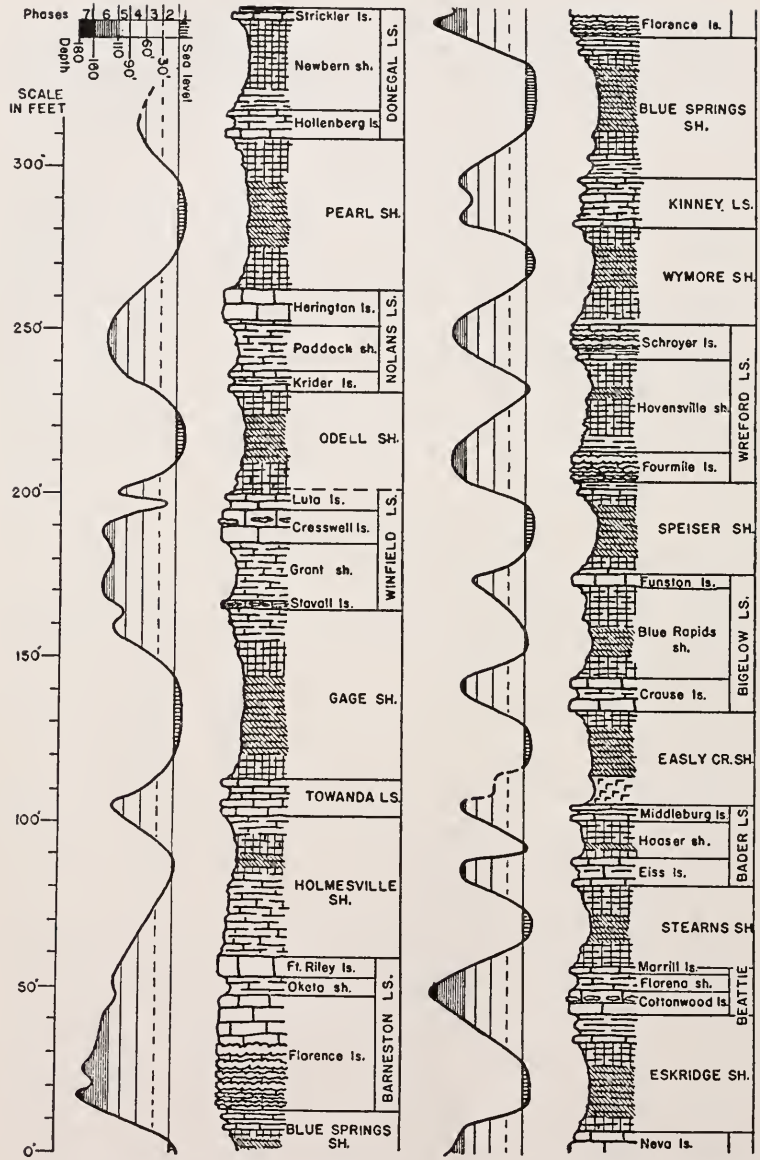

Fig. 1. Composite geologic section of part of the Lower Permian succession in Kansas with accompanying graph showing nonmarine units and inferred depth of inundation in marine units (after M. K. Elias).

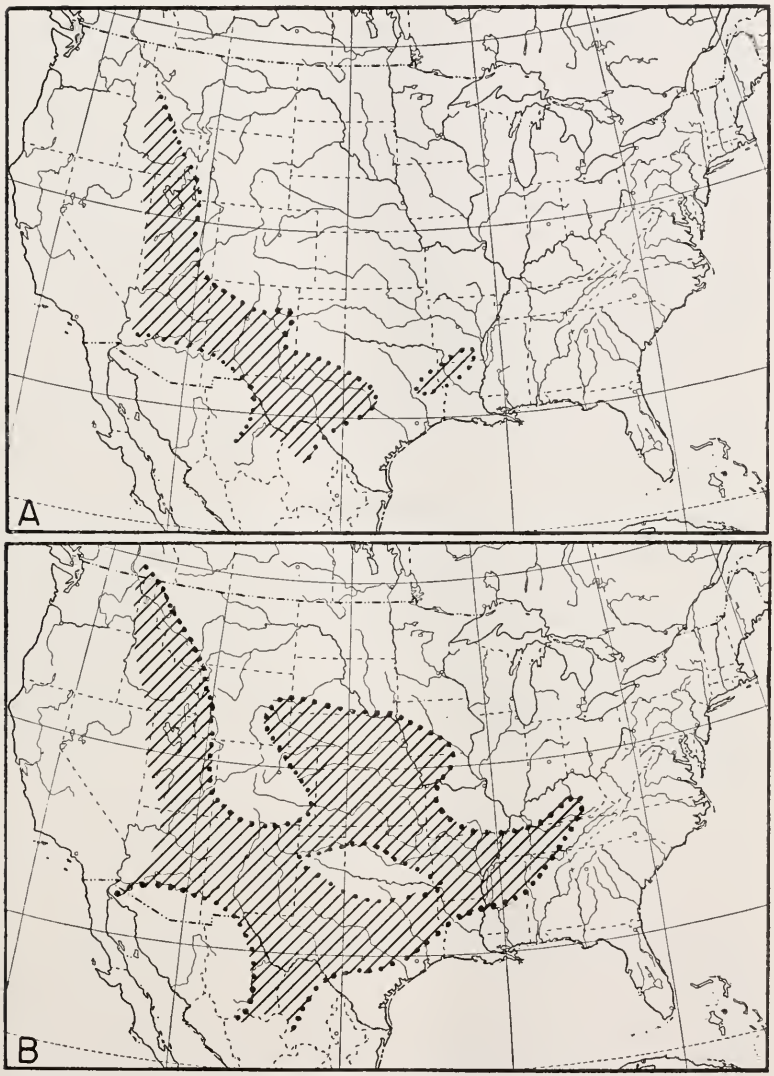

Fig. 2. Paleogeographic sketch maps showing inferred approximate location of seaways during (A) one of the several times of relative continental emergence (when Eskridge deposits were made in Kansas) and (B) the immediately following rather considerable shallow-sea transgression (when fusulinid-bearing Beattie strata were laid down in Kansas).

extent of Lower Permian deposits in the northern midcontinent region have been described in some detail (Condra and Upp, 1931; Jewett, 1933; Moore, 1936-1953; Moore and Thompson, 1949; Moore *et al.*, 1951). Also the nature of faunal associations belonging to different subdivisions of the marine part of cyclic deposits has been delineated and interpreted (Elias, 1937; Moore, 1936, 1949, 1950, 1953). Therefore, discussion here is superfluous, but a part of the Lower Permian succession may be shown graphically (Fig. 1). This is chosen because fusulinids derived from these rocks are employed in a later part of this paper as material for investigation of evolutionary changes.

A method of illustrating the geographic magnitude of shallow-sea oscillations in Pennsylvanian and Permian time in the central United States is by means of paleogeographic maps. Figure 2 presents such maps for two adjoining segments of the Lower Permian succession in the midcontinent region. Taken together, they represent only a very small fraction of Permian time, for Figure 2A represents geographic conditions perhaps only 100,000 years before those depicted in Figure 2B. In early Permian time, the areas successively flooded and laid bare in the central United States were much smaller than in the preceding Pennsylvanian period. Although outlines of the seas shown in Figure 2 are conjectural, they emphasize the point that the marine oscillations affected many thousands of square miles. They should have had an influence on evolution of invertebrate animals living in the shallow seas.

EVIDENCE FURNISHED BY SELECTED INVERTEBRATE GROUPS

General Statement

For the purpose of studying effects of broad shallow-sea oscillations on the evolution of bottom-dwelling invertebrates, any group of them found preserved in a number of successive distinct cycles is appropriate for investigation. Some assemblages are likely to be better than others, however. The chief guides in choosing materials for study are: (1) availability of a reasonably large number of specimens belonging to the group in each of the compared marine deposits, (2) adequacy of fossil collections from precisely known stratigraphic positions, (3) thoroughness

of investigations leading to discrimination of significant morphological and taxonomic interrelations, and (4) distinctness of differences that may be judged ascribable to evolutionary change.

A fairly large sample of an invertebrate group in a specified shallow-sea deposit is required in order to appraise characters that possess value in defining evolutionary trends. Such a sample may be composite, coming from many localities, but it must be representative. Also, each of the two or more compared independent marine units needs to supply materials of this sort, for otherwise comparison leads to dubious conclusions or it is impossible. Genera, subgenera, and possibly species that exhibit at least moderately extended stratigraphic range are the only taxonomic units which can be considered suitable for this study.

Adequacy of fossil collections is a self-evident requirement. Evidence that exists in the field is not usable until it is brought to the laboratory and subjected to careful analysis. In early geological studies, knowledge of detailed stratigraphic relations was lacking generally and its value was unappreciated. Therefore, most fossil collections from late Paleozoic strata in the northern midcontinent region which were made before 1920 have greatly impaired usefulness unless locality records permit accurate identification of the exact source of the fossils.

Comprehensive research of so-called monographic sort is needed before almost any roup of Pennsylvanian or Permian invertebrates can be studied usefully with the object of recognizing evolutionary distinctions and trends. Seemingly, all kinds of benthonic organisms living in shallow seas of the North American continental platform had attained remarkable stability in late Paleozoic time and although faunas are varied and some of them large, their components mostly persist. As result, a Lower Permian fauna may resemble a Lower Pennsylvanian one so closely in a majority of its elements as to be distinguishable only by specialists. Few invertebrate groups have yet been examined thoroughly.

It is recognized universally that invertebrate groups vary enormously, both within themselves and between time-defined segments within almost any single group, in the clearness and rapidity of evolutionary change which is discernible in their geologic history. Linguloid brachiopods furnish examples of un-

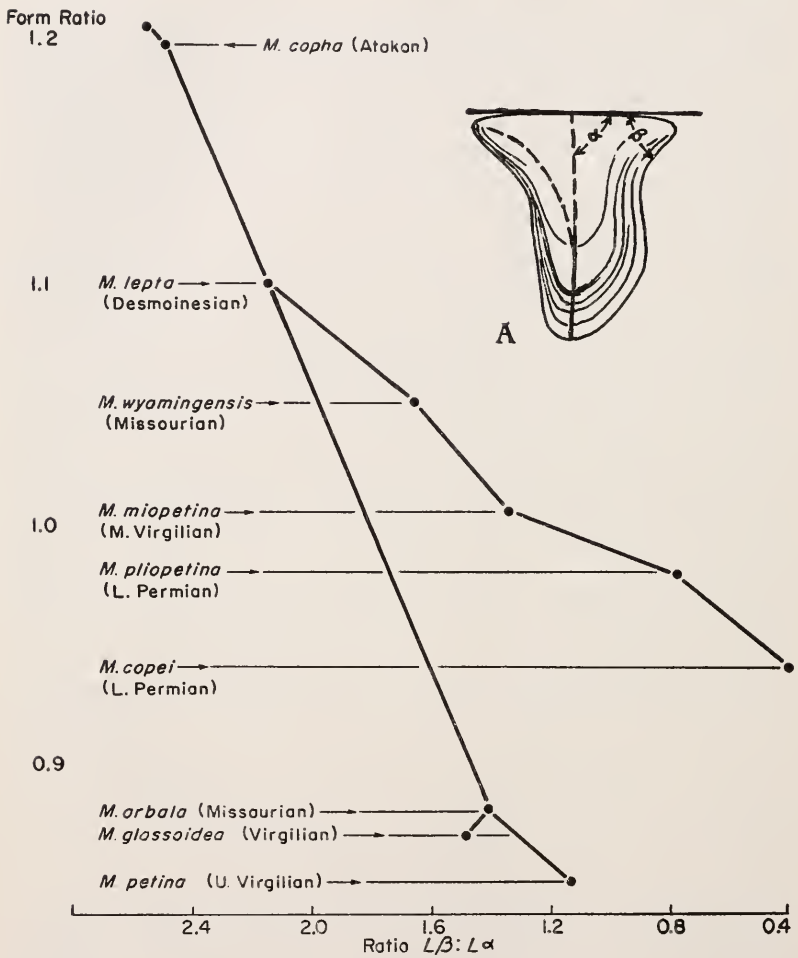

Fig. 3. Evolutionary trends of myalinid shells represented by species from Pennsylvanian and Lower Permian strata of the midcontinent region. The form ratio (shell length to shell height) of species is plotted against the ratio of angle beta to angle alpha (inserted diagram A). Taking account of stratigraphic occurrence, two main trends seem to be derived from *Myalina lepta* of Desmoinesian age (data from Newell 1942).

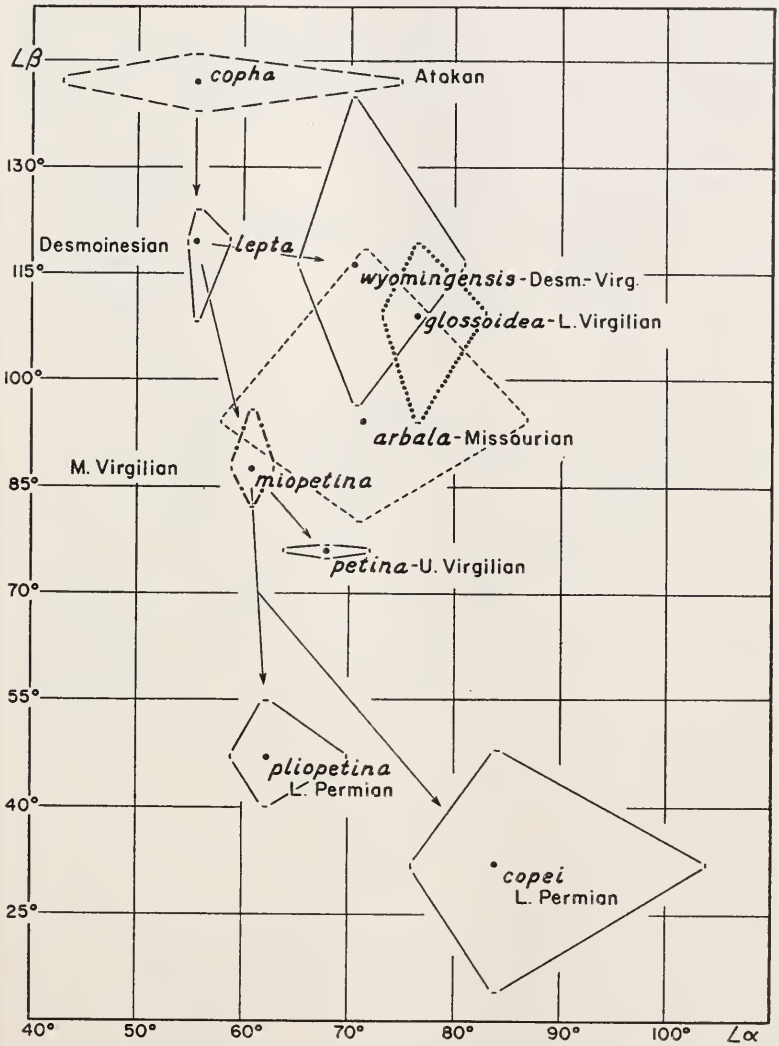

Fig. 4. Range in values (shown by quadrilaterals) and mean values (black dots) of the alpha and beta angles of species of *Myalina* from Pennsylvanian and Lower Permian rocks of the midcontinent region (data from Newell, 1942).

detectable alteration in the course of what must be ten-million-year intervals, whereas the complexly organized crinoids display profound and generally rapid evolutionary change. A satisfactory rating of late Paleozoic invertebrate groups according to

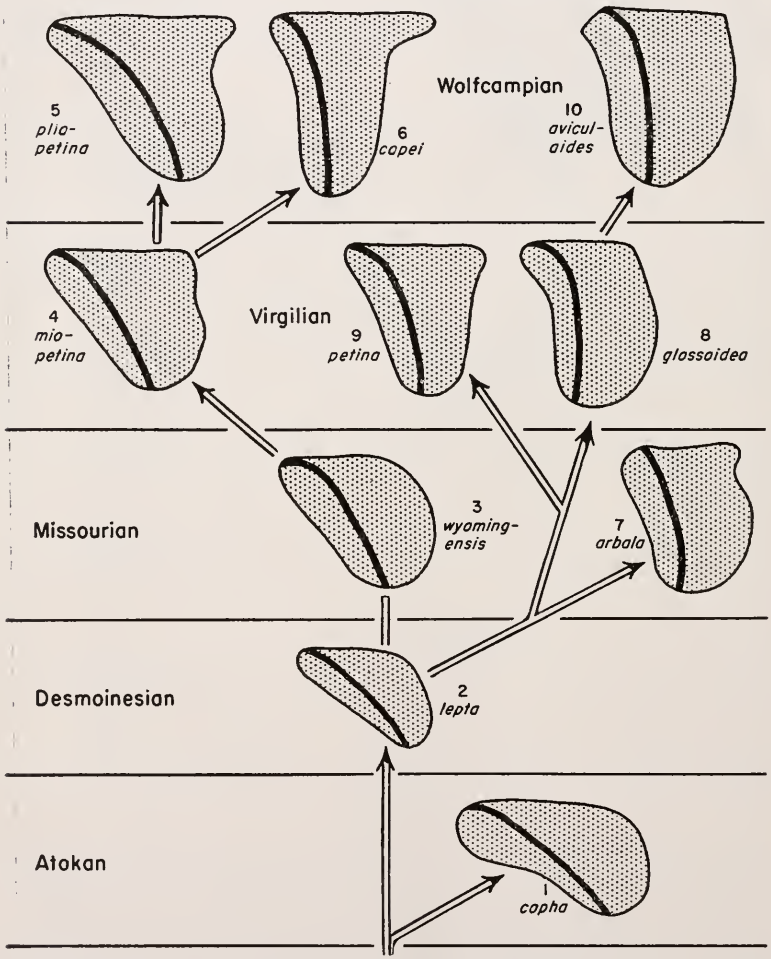

Fig. 5. Inferred phylogenetic relations of some Pennsylvanian and Lower Permian myalinid species from the midcontinent region, based largely on data illustrated in Figures 3 and 4.

distinctness of numerous evolutionary modifications is not now possible, although ammonoids, fusulinids, and crinoids surely would rank high. The fusulinids are a supremely useful group because of their almost incredible abundance, wide geographic distribution, occurrence in nearly every cycle of Pennsylvanian and Permian deposits, and considerable range of morphological differentiation.

In the study here reported, attention was directed to chonetid brachiopods, fistuliporoid bryozoans, myalinid and pectinoid clams, and Lower Permian fusulinids. This choice was based on the availability of monographic studies completed or in progress. Only the myalinids and fusulinids, however, are discussed in this paper.

Myalinid Pelecypods

Pelecypods of the group called myalinids are widely distributed in late Paleozoic near-shore marine deposits of the northern midcontinent region. They are more or less common in nearly every cycle. A comprehensive study of these shells, based on large collections from precisely controlled stratigraphic positions and from very numerous localities, has been made by Newell (1942). His work has led to recognition of ten generic or subgeneric groups in the family Myalinidae and to differentiation of some 30 species of *Myalina*.

Among characters found by Newell to be most useful for classification and recognition of evolutionary trends are shape of the shell, including especially the angle between the umbonal ridge and the hinge line (termed alpha angle) and the similar angle between hinge line and growth lines at the posterior margin (termed beta angle). In addition to a tendency of shells to become larger and thicker in the course of evolution, unidirectional trends in the nature of these angles is observed. Figures 3 to 5 furnish graphic indication of characters of some species belonging to the subgenus *Myalina* (*Myalina*). Evolutionary modifications can be detected and reasonable inferences as to genetic relationships among species can be drawn. The assigned stratigraphic range of most species, however, is too great to allow recognition of differences between specimens found in marine parts of the successive Pennsylvanian and Permian cyclic deposits.

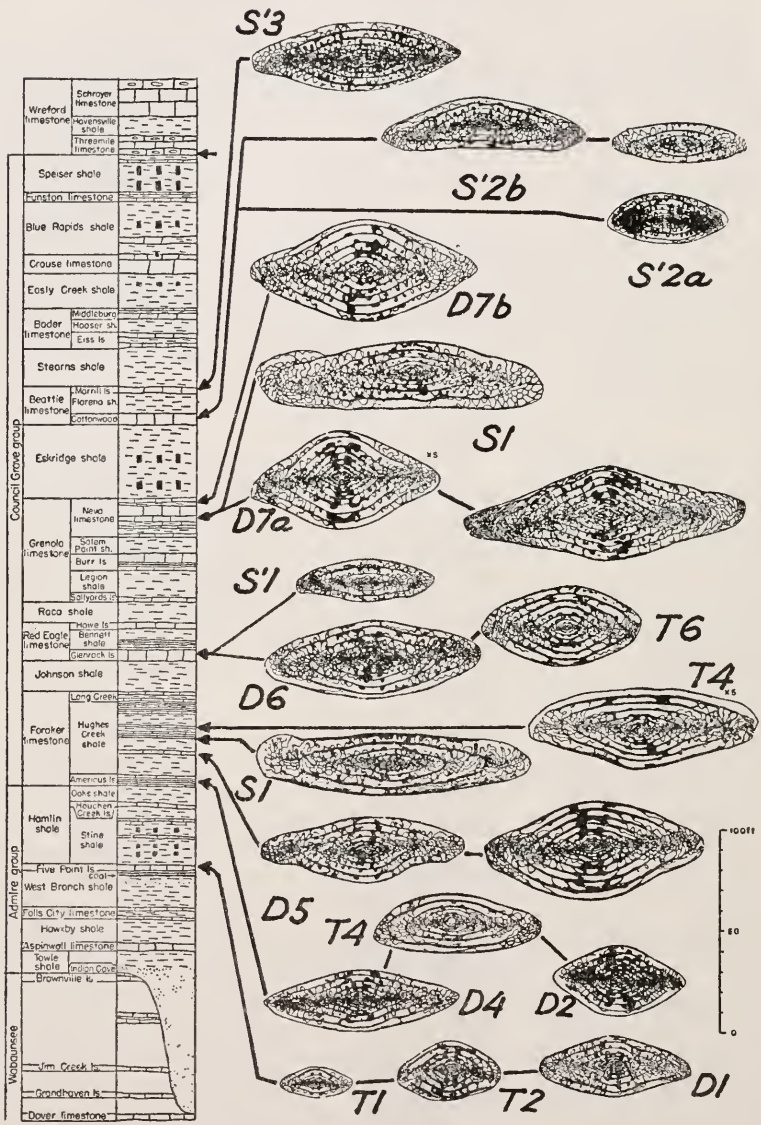

Fig. 6. Generalized section of Lower Permian deposits in Kansas showing longitudinal sections of representative fusulinids from various shallow marine strata (modified from Thompson, 1954).

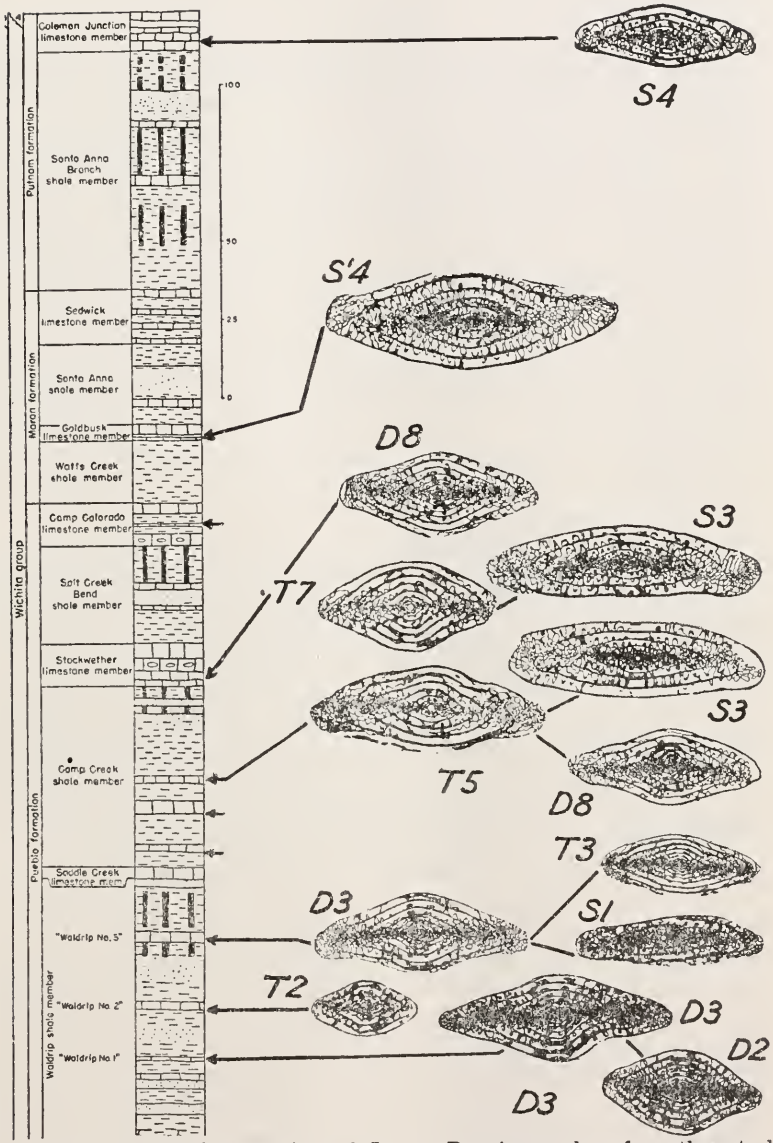

Fig. 7. Generalized section of Lower Permian rocks of north-central Texas showing longitudinal sections of representative fusulinids from shallow marine strata. Heavy vertical bars represent nonmarine red deposits (modified from Thompson, 1954).

Fusulinids

Study of Lower Permian fusulinids as markers of evolution in response to extensive marine oscillations was undertaken because of the completion recently of comprehensive research by M. L. Thompson (1954) on these fossils. Primarily based on collections from Kansas (40 localities) and Texas (47 localities) representing every discovered fusulinid-bearing zone in the Wolfcampian part of the rock column, Thompson's investigation also included very numerous specimens from Oklahoma, New Mexico, Nevada, Utah, Arizona, and California. One new fusulinid horizon (Wreford limestone) has been discovered in Kansas since the time of Thompson's work (D. E. Hattin, personal communication). The monograph by Thompson describes and illustrates 56 species (42 new) which are distributed among 11 genera. The stratigraphic occurrence of all forms is recorded precisely, and accordingly a good source of information is offered for investigation of the sort here discussed.

Cyclic deposits containing fossiliferous marine strata separated by generally unfossiliferous nonmarine beds characterize the Lower Permian succession in Kansas and Nebraska, parts of Oklahoma, and north-central Texas. They may occur in other states also but my attention in the present study has been restricted to the part of Thompson's paper concerned with Kansas-to-Texas fusulinids. These include species which are identified both in the north and south and those recorded as yet only from the Kansas region or from north-central Texas. Figures 6 and 7 show the Lower Permian succession and stratigraphic position of fusulinid-bearing rocks in Kansas and Texas, respectively.

In order to obtain a common denominator for the Kansas and Texas sections, identifying as exactly as possible the equivalent marine rock units in each, two paleontological main tie points are employed. The lower one consists of fusulinids near the base of the northern and southern successions; they include *Triticites confertus* Thompson and *Dunbarinella eoextenta* Thompson, found in both, associated with slightly different but closely related fusulinids (*T. pointensis* Thompson, in Kansas, and *D. extenta* Thompson, in Texas) and other species (*Meekopora prosseri* Ulrich, *M. mollis* Moore and Dudley, and distinctive abundant crinoid ossicles including the so-far-as-known very short-ranged

Triceracrinus Bramlette). The higher tie point is located at the horizon of the Goldbusk limestone in Texas and Florence limestone in Kansas, each of which contains an assemblage of fusu-

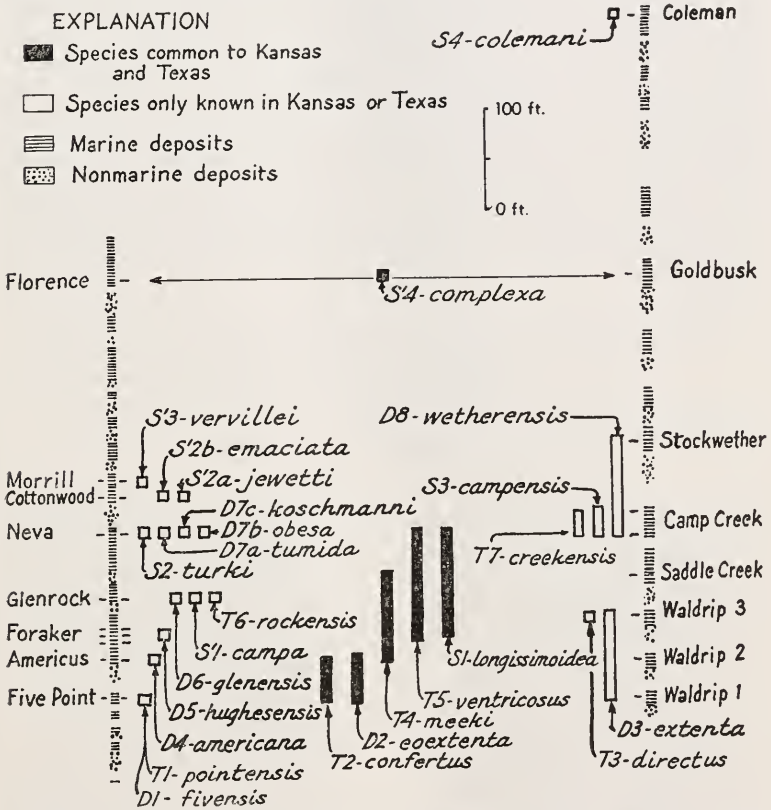

Fig. 8. Stratigraphic distribution of selected fusulinid species in the Kansas and Texas Lower Permian sections. The Florence and Goldbusk fusulinid-bearing strata are judged to be closely contemporaneous for, in addition to *Schwagerina complexa,* they contain *Pseudoschwagerina texana* and *Pseudofusulina? moranensis,* all three species being found in no other rocks of north-central Texas or the Kansas region. Other species found near the base of the Permian deposits in Kansas and Texas indicate age equivalence of these rocks. Thus, an integrated scale in terms of fusulinids can be constructed. (T1-T7, species of *Triticites;* D1-D8 species of *Dunbarinella;* S1-S4 and S'1-S'4, species of two inferred lineages of *Schwagerina*).

linids found nowhere else, although one of the species occurs also in Lower Permian rocks of western Texas and New Mexico. The Goldbusk and Florence species are distinctive forms named *Pseudoschwagerina texana* Dunbar and Skinner (also in Wolfcamp rocks of the Glass Mountains and Hueco limestone of the Sierra Diablo and Hueco Mountains), *Schwagerina complexa* Thompson and *Pseudofusulina? moranensis* Thompson. The strata containing this fusulinid assemblage must be very nearly equivalent in age, if not precisely so. A comparison of the Kansas and Texas sections showing placement of fusulinid species studied in preparing this paper is given in Figure 8 and a tabulation of marine units which tentatively are considered to have the same age follows.

Correlation of Marine Lower Permian Stratigraphic Units in Kansas and North-central Texas

(Units containing identical species of fusulinids marked by **; other fusulinid-bearing units marked by *)

Kansas	*Texas*
Nolans limestone	*Coleman Junction limestone
Winfield limestone	Sedwick limestone
**Florence limestone	**Goldbusk limestone
*Wreford limestone	*Camp Colorado limestone
*Beattie limestone	*Stockwether limestone
**Neva limestone	**Camp Creek shale (and limestone)
**Glenrock limestone	**Saddle Creek limestone
**Foraker limestone (Hughes Creek)	**Waldrip shale (No. 3 limestone)
**Foraker limestone (Americus)	**Waldrip shale (No. 2 limestone)
**Fivepoint limestone	**Waldrip shale (No. 1 limestone)

Comparison of fusulinid species belonging to any given generic assemblage with the object of distinguishing evolutionary trends naturally must take account first of relative age of the chosen fossils. Older forms may have given rise to younger ones but not the reverse. Morphological features must be examined in order to discover resemblances and differences. Average size of

individuals is not likely to be significant, although this may be a specific character along with others. Nearly all descriptions of fusulinid species are accompanied by more or less extensive tables of measurements which furnish record of observations concerning not only the whole shell but the proloculus and each successive volution. These data constitute a statistical delimitation of various morphological elements but it is difficult indeed to use them directly in making comparisons and in learning what may be most significant. Graphic analysis of such information rarely is given by authors and therefore a good deal of time was spent by me in trying to plot useful graphs. Some showed average measurements or computations and others showed values reported for individual specimens, thus indicating range of variations. Ratios of two selected characters recorded by measurements can be plotted against a third set of measurements or against other ratios. Some work along this line seemed to be worth while but most of it was discarded.

Triticites

A somewhat arbitrarily chosen but seemingly useful starting point for the comparative study of fusulinid species consists in plotting average measurements for the diameter and wall thickness of the proloculus. Among Lower Permian species from Kansas and Texas described by Thompson, the proloculus diameter is found to range from less than 100 to nearly 250 microns and the wall thickness from 9 to 25 microns (Fig. 9).

If the stratigraphically lowest species is postulated to be ancestral (or alternatively, closely similar to ancestral) to younger species found higher in the section of Kansas, Texas, or both, a line or lines drawn from the plotted point for the oldest species to points representing other species indicates the nature of evolutionary trends. The premise that evolutionary trends are consistent, rather than erratically reversible, underlies the conclusion that not all observed species belong to a single chain between the presumed progenitor and its youngest known descendant. Rather, the directions of evolutionary alteration may diverge from a parent stock so that graphic representation of inferred relationships has a branched pattern, as in Figure 9.

It is obvious that an inherent assumption in the procedure

just described is that all of the forms considered are actually interrelated, all being derived from a source consisting of the oldest species of the group. The validity of this assumption is open to challenge, since one or more of the studied species may be immigrants to the Kansas or Texas areas, being derivatives of stock that resided in some "foreign" part of the Permian shallow seas such as New Mexico, Arizona, or Utah. Also, if *Triticites rockensis* Thompson from the Glenrock limestone of Kansas) is a lineal descendant of *T. pointensis* Thompson or *T. confertus* Thompson, found in stratigraphically lower marine

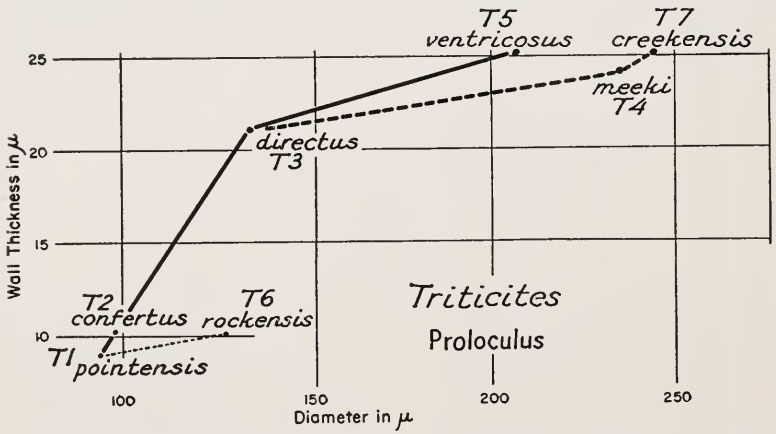

Fig. 9. Proloculus of species of *Triticites* plotted according to diameter and wall thickness. Taking account of stratigraphic occurrence, three different lineages are suggested. The letters T1-T7 inclusive correspond to those shown in Figure 8.

deposits of Kansas, and if the line of descent to *T. rockensis* does not include *T. ventricosus* (Meek and Hayden) or *T. meeki* (Möller), which occur in Kansas rocks older than the Glenrock limestone, a question is raised concerning the identity and place of occurrence of immediate forerunners of *T. rockensis*.

Figure 10 illustrates morphological characters (form ratio, height of chambers, thickness of spirotheca, cumulative number of septa, and tunnel angle) of the Lower Permian species of *Triticites* from Kansas and Texas as measured at the fifth volution, lines being drawn between plotted points for the individual

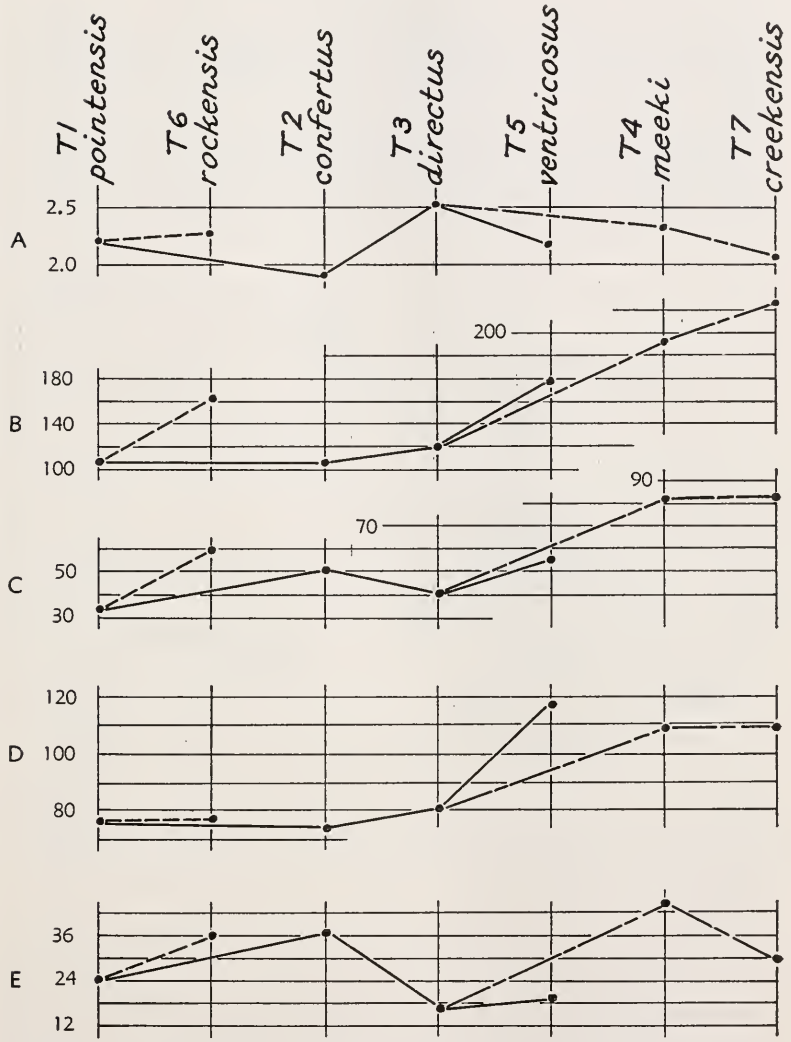

Fig. 10. Morphological features of the fifth whorl of Lower Permian species of *Triticites* arranged according to lineages suggested by Figure 9 (A, form ratio; B, height of chambers; C, thickness of spirotheca; D, number of septa, cumulative to end of fifth whorl; E, tunnel angle.

species in a manner corresponding to that in Figure 9. Graphs which were constructed similarly for all volutions do not differ enough from the one presented here to warrant publication of them.

Average values for form ratio (Fig. 10A) are almost the same in *Triticites pointensis* and *T. rockensis* but show ups and downs along the lines leading to other species. This suggests that form

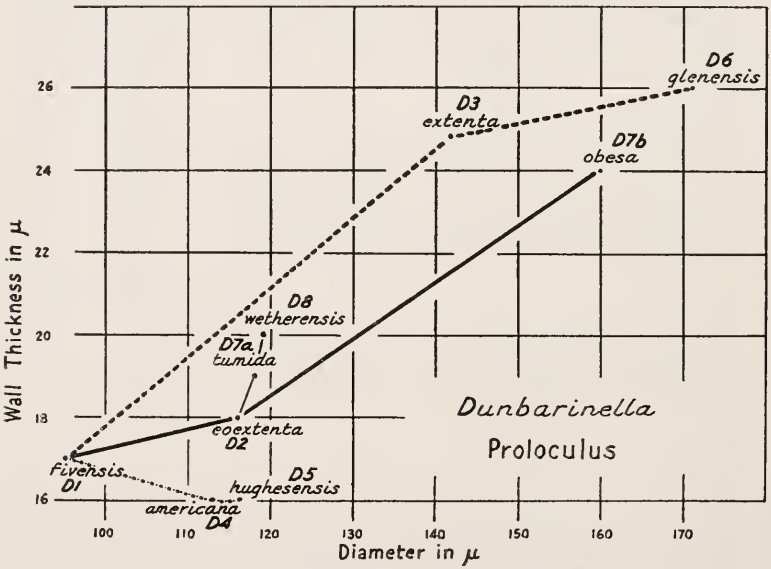

Fig. 11. Proloculus of Lower Permian species of *Dunbarinella* showing diameter and wall thickness. Taking account of stratigraphic occurrence, three lineages of these species are suggested. The letters D1-D8 inclusive correspond to those in Figure 8.

ratio is not a very reliable indicator of evolutionary change because it moves in reverse directions or else the compared species are not actually a genetically related series. The same inference is appropriate in trying to interpret the graph of tunnel angles (Fig. 10E). On the other hand, comparison of values for chamber height, thickness of spirotheca, and number of septa (Fig. 10B-D) plausibly conform to a pattern of evolution having consistent trends.

Dunbarinella

Studies of the Kansas and Texas species of *Dunbarinella* described by Thompson (1954) were made in the same way as for *Triticites*. Graphic representation of proloculus characters (Fig. 11) suggests existence of four lines of development, but attention needs to be called to the record of *D. eoextenta* Thompson asso-

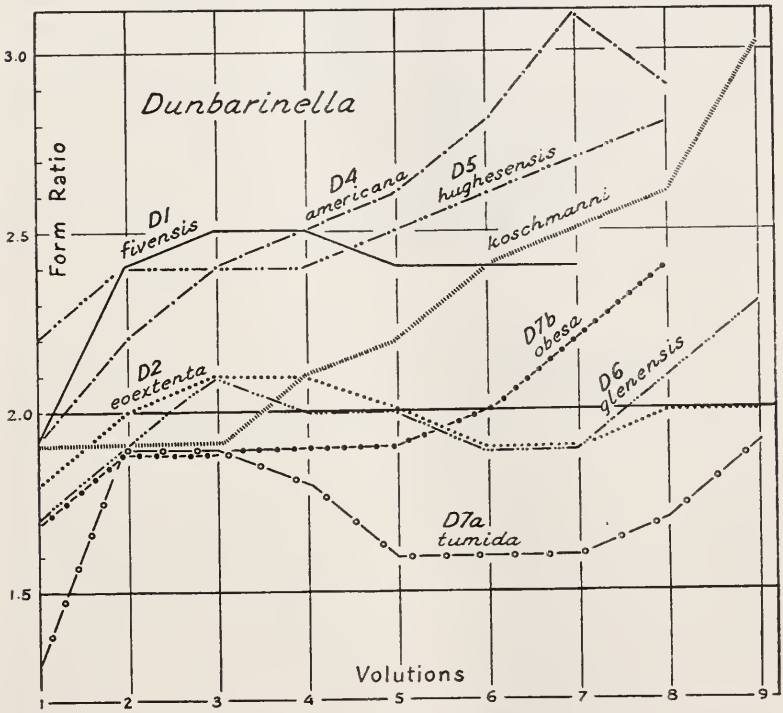

Fig. 12. Form ratios of Lower Permian species of *Dunbarinella* showing variation during growth.

ciated with *D. fivensis* Thompson in the Fivepoint limestone of Kansas and the presence of both *D. eoextenta* and *D. extenta* Thompson in rocks of the same or nearly identical age in north-central Texas. Thus, these three species which have notable differences in character of the proloculus are contemporaneous at least in part; because they have other features that indicate close

relationship, it is probable that they are slightly divergent derivatives of a late Pennsylvanian ancestor. In wall thickness and diameter of the proloculus, *D. extenta* rivals the stratigraphically higher *D. glenensis* Thompson and *D. obesa* (Beede).

In order to illustrate ontogenetic changes, as well as the range of variation among the studied species of *Dunbarinella*, the values of computed form ratios for each volution have been plotted (Fig. 12). They show that conclusions based on comparison of a single growth stage may not be reliable. Since similar graphs of other characters mostly demonstrate acceleration or retardation in the rate of change from volution to volution, they offer little indication that successive growth stages furnish record of the course of phylogeny. Diagrams prepared in the manner of Figure 12 seem to be useful for summarizing taxonomic aspects of morphological features but they fail to indicate directly the nature of evolutionary trends which otherwise may be discernible in the group of species.

Comparison of morphological characters of species of *Dunbarinella*, based on measurements of the sixth volution, which is nearest to the adult stage as far as data for all species are available, is shown in Figure 13. The line connecting *D. fivensis* with *D. americana* Thompson and *D. hughesensis* Thompson and that joining *D. fivensis* with *D. extenta* and *D. glenensis* are both consistent with evolution in fairly uniform though divergent directions. On the other hand, indicated trends from *D. fivensis* through *D. coextenta* to *D. tumida* (Skinner) and *O. wetherensis* Thompson, and less clearly to *D. obesa* (according to the pattern suggested by Figure 11) seem to be anomalous. *D. tumida* and *D. obesa*, which occur with *D. koschmanni* (Skinner) (Figs. 8, 12, 13) in the Neva limestone of Kansas and northern Oklahoma, are conceivably derivatives of the older *D. eoextenta* but not from the also older *D. americana* and *D. hughesensis* group or the *D. extenta* and *D. glenensis* group. That some of these species are interlopers of unknown origin, rather than descendants of indigenous midcontinent species, is very possible. The wide range in values of measurements representing most morphological elements is a noteworthy feature of these fusulinids, leading one to think that recognition of definite evolutionary trends should be relatively easy. Such is not true.

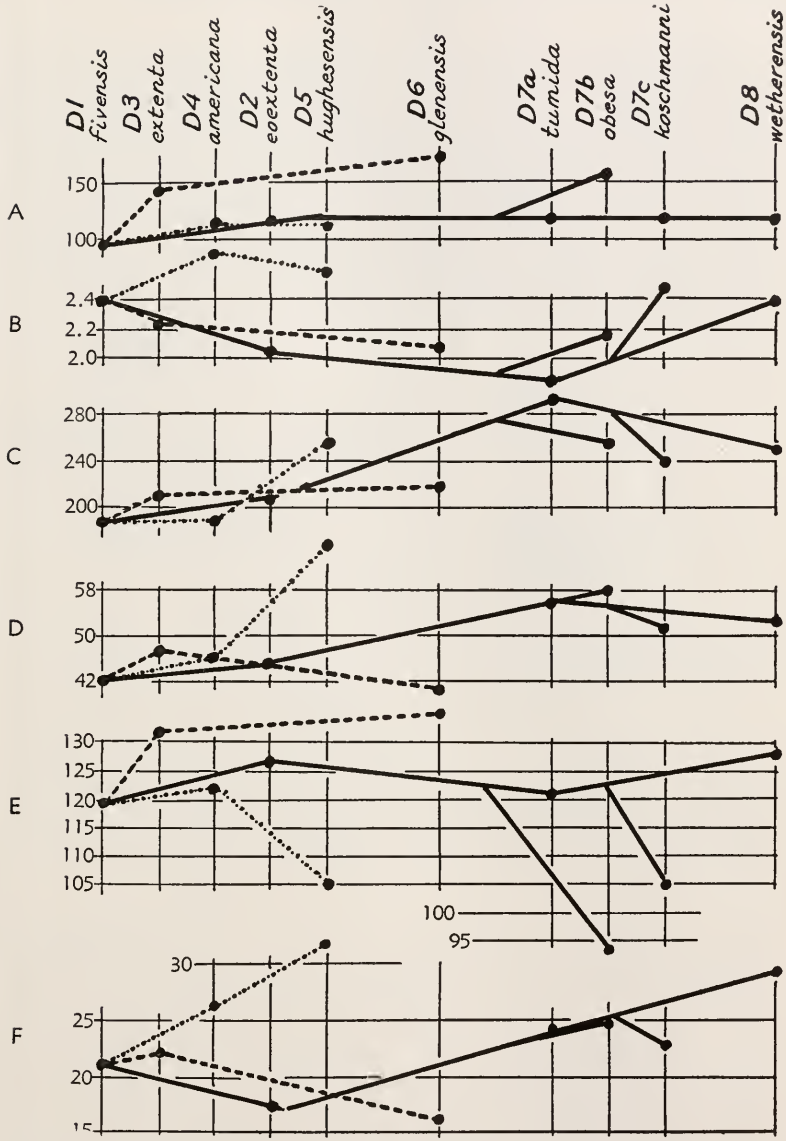

Fig. 13. Morphological features of Lower Permian species of *Dunbarinella* with differentiation of inferred lineages as shown in Figure 11. A, indicates diameter of the proloculus (in microns). B to F represent characters of the sixth whorl (B, form ratio; C, height of chambers, in microns; D, thickness of spirotheca, in microns; E, number of septa to end of sixth whorl; F, tunnel angle, in degrees). (Data from Thompson, 1954.)

Schwagerina

Another Lower Permian genus which is represented by numerous species (10 in the midcontinent area and 9 others from trans-Pecos Texas and country farther west) is *Schwagerina*. Characters of the proloculus (Fig. 14) suggest division of the midcontinent forms into two sharply distinguished groups. These respectively comprise *S. campa* Thompson, *S. jewetti* Thompson, *S. vervillei* Thompson, *S. emaciata* (Beede), and *S. complexa* Thompson in one assemblage and *S. longissimoidea* (Beede), *S.*

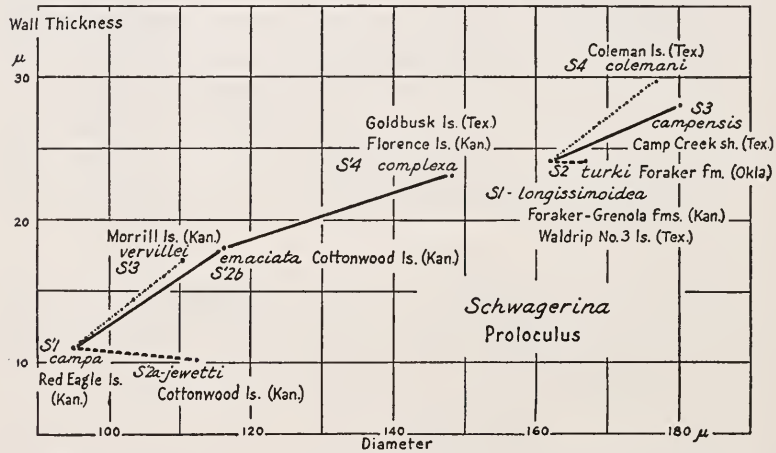

Fig. 14. Proloculus of Lower Permian species of *Schwagerina* showing diameter in relation to wall thickness. Taking account of stratigraphic occurrence, two groups of divergent lineages are suggested. These are marked by letters S1-S4 and S′1-S′4, respectively, corresponding to notations on Figure 8.

turki (Skinner), *S. campensis* Thompson, and *S. colemani* Thompson in the other. As shown by Figure 14 and also by plotted measurements of various morphological features (Fig. 15), it is reasonable to suggest that the group containing *S. campa* is based on this species as origin, whereas the group containing *S. longissimoidea* was derived from this species. Studies which I have made are insufficient to warrant postulates concerning the common origin of the two assemblages or that of the genus, but the oldest known representative (*S. longissimoidea*) in

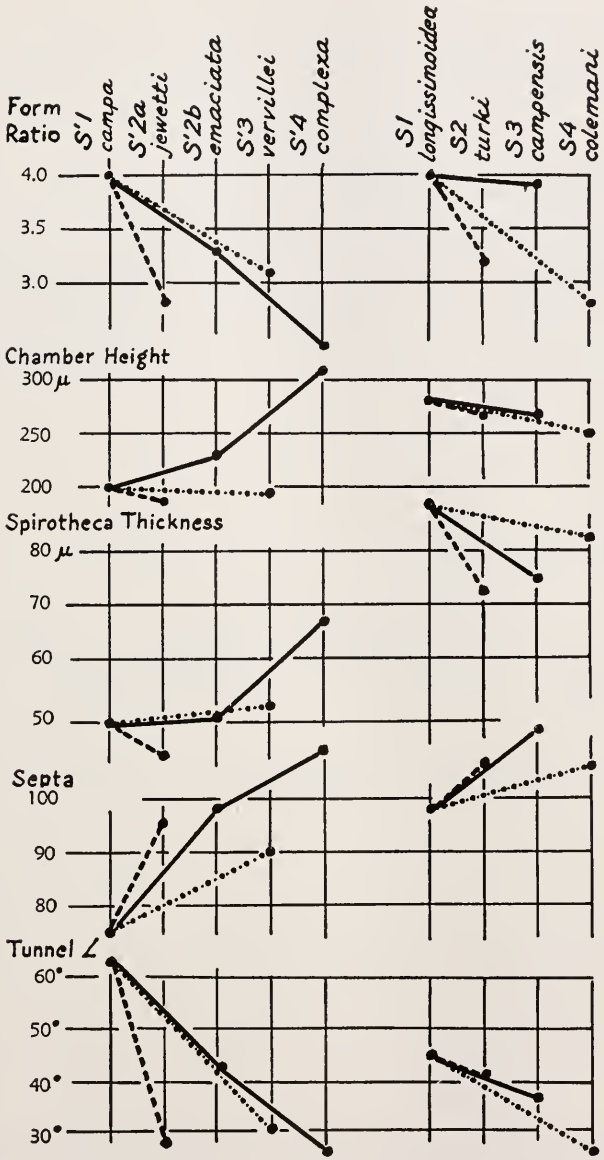

Fig. 15. Morphological features of Lower Permian species of *Schwagerina*, all representing growth stages at end of the fifth volution. Septal counts are cumulative, including volutions 1-5 (Data from Thompson, 1954).

the midcontinent is rather surely not the form sought. The *S. campa* group of species exhibits structural characters and trends that are unrelated to those of the *S. longissimoidea* assemblage.

CONCLUSIONS

Comparative study of marine invertebrates preserved as fossils in successive cyclic deposits of late Paleozoic age in the central United States is a very promising type of research for evaluation of the effects on evolution of broad oscillations of shallow seas which in relatively short spans of geologic time alternately inundate and then uncover large parts of continental platforms. Investigations of this nature may be undertaken profitably on deposits of Chesteran (late Mississippian) age as well as in Pennsylvanian and Permian parts of the rock column.

Fossils adapted for this study are somewhat narrowly defined taxonomic groups which are well represented in each of several succeeding cycles and which are suited by the nature of their morphological characters to receive a clear impress of evolutionary changes. Generally speaking, the best groups are those having rather complex structural organization and those which are not too specialized by reason of adaptation to a narrow ecologic niche. Large collections of fossils from precisely known stratigraphic positions must be obtained and thorough taxonomic investigation of the selected groups is needed. Statistical analysis, preferably accompanied by graphic treatment of measurements and computations, may aid in the possibly arduous task of finding most significant directions of evolution. Interpretation of the accumulated observations is likely to be less difficult.

A chief question encountered in work on this problem relates to recognition of true lines of descent, for the occurrence of more or less similar species in the marine parts of successive cycles does not prove that the younger is derived from the older. Effects of migration must be taken into account and, depending on circumstances that may be almost wholly conjectural, these effects can be judged to obscure or obliterate evidence otherwise interpreted to signify evolution of indigenous stocks.

Observations on the distribution and nature of species belonging to the pelecypod subgenus *Myalina* (*Myalina*) serve to define evolutionary trends but evidence is insufficient to establish per-

ceptible changes in species from one Pennsylvanian or Permian cycle to the next.

The fusulinid genera *Triticites, Dunbarinella,* and *Schwagerina,* represented by numerous species in Lower Permian cyclic deposits of Kansas, Oklahoma, and north-central Texas, seem to reflect influences of shallow-sea oscillations in the midcontinent region, as shown by analysis of shell characters of forms found in successive cycles. In each genus, divergent trends are seen but interpretation of some species is uncertain because they may be immigrants from distant parts of the Permian sea rather than lineal descendants of forms found lower in the rock section of Kansas or Texas.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 3 October, 1954

Status of Invertebrate Paleontology, 1953
XI. *Systematic, Paleoecologic and Evolutionary Aspects of Skeletal Building Materials*[1]

By H. A. Lowenstam
California Institute of Technology

Skeletal remains of organisms constitute the common records of bodily preserved components in the sedimentary sequences of the earth's crust. Paleontology, as of to date, has been predominantly occupied with the study of skeletal types of records. The initial task has been, and for this matter still is, to canvass these biologic records and to place them into the broader framework of the recognized levels of increasing complexity and to relate them to others within these, in order to chart the course of phylogenetic changes through geologic time. With the increase in knowledge of the principal types of organic representatives with preservable skeletons through the time succession, interpretive aspects of the meaning of evolution (based on a better understanding of the mechanisms of dynamic changes, largely through genetic concepts) have progressively become the focal point in the synthesis of the paleontologic records. With recognition of the screening effects of the environmental framework (apart from the controls exerted by the interrelations of the biota as a whole, i.e. the channeling mechanism of evolutionary processes), ecologic factors have become of increasing concern in the paleontologic inquiry. The approaches here were directed toward discerning skeletal expressions in adaptive, functional morphologic terms and to integrate these with environmental expressions of the enclosing sedimentary rocks, wherever living and burial grounds were assuredly coincidental or closely related. The expressions of concern were largely physical in nature, as observed in the macro- and micro-architecture of the skeletal records or physical expressions of chemically induced morphologic changes. This is best shown by the factors of concern in the paleoecologic investigations of marine fossil assemblages, e.g., turbulence, turbidity, depth of water, bottom consistency, salinity, and temperature, all

[1] Publications of the Division of the Geological Sciences, California Institute of Technology, Pasadena, California, Contribution No. 700.

of course in relative terms. For instance, regarding the detection of physical expressions of a chemical environmental effect, such as that of salinity, criteria of marginal (either hypersaline or brackish water) conditions were deduced by analogy with present day representation in the changes effecting shell morphology of pelecypods in the form of dimensional distortion, thickness and size reductions.

In recent years, there has been a rapid improvement of earlier established techniques and the development of new ones in the field of X-ray mineralogy, and in trace element and isotope chemistry which in their applications have been concerned incidentally or specifically with recent and fossil skeletal building materials. These have demonstrated that skeletal mineralogy constitutes, potentially, a supplementary source vector of anatomic-physiologic and ecologic information; this knowledge, through integration with that of physical aspects of morphology and sediment-derived information, promises not only to strengthen interpretational aspects, but also to aid in quantifying previously qualitatively-evaluated parameters. There are further indications that such applications will widen the scope of the paleontologic inquiry, beyond the range of morphologically-derived information amenable to analyses in the morphologic area, to physiologic aspects and hence will reveal phases of biochemical evolution. Progress and scope of the inquiry in this area will depend equally if not to a greater extent upon information derived from biochemical studies of organic remains and their degradation products in the fossil records, already under scrutiny (Abelson, 1954).

The investigation of biologic properties by biogeochemical means must be evaluated, and procedure is initially determined by a number of considerations. The basic concerns are the principles governing the inorganic processes of precipitation and the isotope chemistry of inorganic precipitation of the crystal types that constitute skeletal hard parts (or, where organic matrices are initially elaborated, their strengthening agents), and also the trace element uptake levels by the respective host minerals. As organisms constitute the synthesizing agents of skeletal crystalline matter, the framework of reference of the crystal chemical precipitation and activity levels over the range is controlled by such determining factors as those related to biologic tolerances

(which vary as a function of a given species and with reference to their ecologic valence), the response characteristics, and the degree of environmental dependence of the species upon the activation of the skeletal secretionary processes. Next, from the paleobiologic point of view, one should consider, after thorough diagnosis of the enclosing sediments, the stability relations of the original skeletal mineralogic compounds, their isotopic ratios and trace element concentrations over the range of differing physical-chemical environments through which the skeletal mineral components have passed (from the moment of burial under similar conditions to quite different ones).

The primary level of background information on the fundamental physico-chemical and isotope chemistry concepts in their development concerns us as paleontologists only insofar as it may be applied to obtaining information on biologic aspects. The second level of background knowledge, the investigation of the principles of the channeling effects of the biochemical catalysts in their expressions in the secretionary products of the skeletal crystal aggregates, lies basically in the domain of neobiologic inquiry. Contrary to the consideration of morphologic aspects, where replacement of e.g., calcitic skeletons by calcium phosphate or silica compounds such as low temperature crystobalite or quartz, is of no concern as long as it does not affect macro- or micro-architecture (whichever may be critical), the biogeochemical investigation is at present confined to entirely, or in part, unaltered skeletal remains. The task at the third level which is assigned to paleontology would then seem to pertain initially to applying the principles evolved by neobiology to the investigation of the stability ranges of the skeletal crystal chemicals and their trace element and isotopic properties with reference to each individual character and by crystal characteristics within each of the skeletal-bearing groups. The aspect of concern here is primarily to find criteria to recognize where post mortem changes have taken place, and to avoid erroneous interpretations of the history of origin as it reflects the environmental framework. Properly screened by distinguishing differences of ecologic from evolutionary changes, it should then be possible to chart the course of phylogenetic changes in skeletal secretionary processes and their contribution to the modes in evolution. The disadvan-

tageous position of paleobiology with reference to neobiology is to be confronted with fragmentary remains of organisms; one must then place emphasis on searching always for criteria of correlation of biologic and ecologic properties which lie in the range of what may be potentially preserved in the fossil remains. This may restrict the consideration of paleobiology not infrequently to second or third order expressions of phenomena in organic components which seem preservable but of little concern and, hence, not correlated by the neobiologist as long as they are obscure, by comparison with obvious though not preservable expressions. It is thus not a coincidence that in the investigation of physical properties that, for instance, denote ecologic expressions, the ranges of criteria which are amenable to paleontologic research have commonly been and are still being extended by paleoecologists rather than by neoecologists from observations of skeletal characteristics of present-day biota. In the area of skeletal biogeochemistry the situation is even more acute in that information fundamental to the definition of principles is highly unsatisfactory. Hence, to utilize basic knowledge accumulated on the first level and apply it to the third level, that is, to paleobiology, the principles on the second level must first be developed. It is for this reason that consideration of skeletal mineralogy and trace element chemistry is at present preoccupied almost entirely with aspects of present-day organisms.

It is the purpose of the following to elaborate the results of biogeochemical studies on calcium carbonate skeletons. The writer has participated in such studies as oxygen isotope method of temperature determinations with reference to ecologic factors and evolutionary aspects and has investigated aragonite-calcite relations to environmental factors and certain aspects of trace element chemistry in relation to temperature. Temperature effects can be detected in some carbonate skeletal types by O^{18}/O^{16} ratio, the calcite-aragonite ratio and trace element concentrations. The best documentation of the trace element relation with reference to temperature has been worked out by Chave (1954) for the magnesium content of carbonate skeletons and hence consideration is given to his work. The potential application of three independent sets of criteria for temperature determinations is, from the methodological point of view, encouraging, as it will tend to re-

duce erroneous temperature determination. The oxygen isotope method and the magnesium concentration scales allow quantitative temperature determinations. As such they constitute refinements of means of investigations beyond our previous qualitative evaluation of this property. Integration with independently arrived source data of the sort to be pointed out in connection with the paleo-temperature method, reveals the contribution which can be made through biogeochemical studies, and stresses the fact that only if integrated with all sources of basic data will they then become meaningful.

OXYGEN ISOTOPE TEMPERATURE DETERMINATION

The isotope method of temperature determination derives its information from carbonate skeletons of marine organisms (Urey, 1948). It is basically then a biologic tool dependent initially upon groups of organisms which lay down their skeletal carbonate in isotopic equilibrium with that of their surrounding waters (Lowenstam, 1948). These groups must be determined from examination of the spectral range of present-day carbonate-secreting forms. The relations of the range of skeletal secretion to that of the yearly amplitude in temperatures of the inhabited waters must next be clarified. Specifically, it is then an ecologic tool designed to define the skeletal secretionary range for a given species and compare it with biotope associated elements — a parameter to date little investigated. From this it follows that the initial test is to lay a foundation of comparative data on the skeletal secretionary-temperature relations in present day biota where the climatic amplitudes are known. With this as a background it should then be possible to investigate skeletal paleotemperatures of fossils, in which the original isotopic abundances have remained unaltered. This raises the question as to the types and numbers of burial-associated biotic elements which can be employed for paleotemperature determinations and also how far back in geologic time these may be found. In turn, this knowledge can be employed to evaluate the climatic conditions under which the organisms lived.

The present state of information obtained for each of the phases indicated as vital prerequisites to the paleotemperature investigation is as follows. Regarding the question of the group-distribu-

tional spread of present-day organisms which lay down skeletal carbonate in isotopic equilibrium with that of the inhabitant waters, these groups have been shown to be species examined from among the foraminifera, hydrozoans, bryozoans, amphineurans, gastropods, pelecypods, and cephalopods (Urey *et al.*, 1951, Emiliani and Epstein, 1953, Epstein and Lowenstam, 1953, Emiliani, 1954, Lowenstam and Epstein, 1954). Thirty-eight Recent species of the inshore water biota from Bermuda, including in group distributional terms some representatives of foraminifera, hydrozoans, and bryozoans, but centered on the molluscans, served as models to investigate the relations of skeletal secretionary behavior with reference to environmental temperatures (Epstein and Lowenstam, 1953). The yearly amplitude in water temperatures at Bermuda extending from 16°C to 30°C was found admirably suited for comparative study of this particular aspect. Average skeletal growth temperatures determined from representatives of each of the thirty-eight species were found to extend from 18.1°C to 29.1°C, with the density clustering in the range from 23° to 24°C. The average skeletal growth temperature of from 2 to 6 individuals of the same species but from different micro-environments was found to vary within 2°C or less. Comparison of the average shell-growth temperature of the numerically-more-thoroughly-investigated pelecypod and gastropod species, by integral temperature intervals, indicates class-characteristic-frequency groupings for the pelecypods between 23° and 24°C, and for the gastropods between 20° and 22°C. The data are as yet too limited to justify the generalization that class distinct shell-secreting behavior is involved. However, the aspect which did forcibly emerge from limited range in temperature variations per species as contrasted with the overall range in average temperatures by species when all are examined *in toto,* is that skeletal-secreting processes are species-controlled . The meaning of species-determined differentiation in temperature recording was investigated further by means of cross-sectional studies of shells of the pelecypod *Chama macerophylla* with an average shell growth temperature of 23.6°C and of the gastropod *Strombus gigas* with a shell growth temperature of 21.7°C. The results for *Chama macerophylla* showed shell depositional temperatures lying above 21°C throughout. Considering, on the basis of the

irregular temperature fluctuations, the possibility of recurrent partial dissolution and redeposition with the latter process dominant during the warm part of the year, this does not alter the fact that the depositional balance is confined to the elevated temperatures of the yearly range. By contrast, *Strombus gigas* showed rhythmic fluctuations of shell growth temperatures extending over all but the opposite extremes of the yearly temperature range, hence depicting fairly accurate seasonal temperature variations of the inhabiting waters. Considered in terms of the implications of the cross-sectional seasonal temperature studies of these two forms, the comparison of average skeletal temperatures of the scatter range near that of *Strombus gigas*-inferred species with skeletal temperature recordings essentially throughout the year, while those near that of *Chama macerophylla* are confined in their recording range to the warmer temperatures of the yearly amplitude. The highest determined mean average temperatures such as, e.g., the ones of the sessile reef-dwelling *Homotrema rubrum* (27.2–29.1°), imply even more rigorous temperature-time range restriction in deposition as compared with *Ch. macerophylla*, those determining the lower end of the temperature range probably corresponding to the restriction or preferential deposition during the cold part of the year. The latter aspect of temperature-determined-volume-secretionary rates, and also the age of the individual with reference to the yearly climatic range, must enter into consideration and is probably contributory to the distributional scatter of the average-growth temperature observed. Evidence had accumulated for some time, mostly from study of recent pelecypods, that shell secretion becomes discontinuous or at least greatly retarded during the reproductive period, during unfavorable weather conditions such as storm periods, and in the temperate and arctic waters during hibernation in winter, e.g. through species and ecologically determined factors. Compared with the qualitative nature of these data the Bermuda study has demonstrated the value of the isotope temperature methods as a quantitative tool to investigate skeletal depositional relations. Most critically, it has established that there is sharp differentiation by species of the threshold limits of the secretionary range of skeletal carbonate. Illustrated by the example of the tropical species *macerophylla*,

which occupies reproductively a marginal ecologic niche in the shore waters of Bermuda, the skeletal secretionary range as apparently determined by environmental temperatures is restricted as compared with the climatic and climatic-reproductive tolerance range of the species. This then constitutes a refinement in extending the range of ecologic parameters for a given species to the skeletal secretionary processes, which in Recent forms can, of course, be determined also by systematic observational means. From the paleoecologic point of view, the primary significance lies in the fact that this has been the first method developed which makes it potentially feasible (and it has been demonstrated) to obtain information on this particular parameter in the fossil record. In consequence, the method potentially opens the way to charting evolutionary changes in skeletal secretionary behavior with reference to environmental temperatures in lineages. The information may further aid in such cases where habitat-restricted-ranges become evident with time, from zoogeographic studies, to determine whether the skeletal-secretionary-range relations with environmental temperatures indicate preadaptations with reference to the restrictive drift or shifts, which in turn may contribute towards the evaluation of the genetic relationships of lineages where such are open to question.

The degree of differentiation in skeletal-secretionary behavior and the common incidence of this phenomenon in the Recent Bermuda biotic elements examined center the orientation of the method of approach in the paleobiologic inquiry where the climatic amplitudes (against which the recording ranges of skeletal carbonate are measured) are unknown. The nearly complete climatic range obtained (from the sum total of average growth temperature of a large number of species from different classes) indicates that this approach should then lead in paleotemperature studies, to defining climatic amplitudes more likely averaged over the length of time involved in the fossil samples examined, hence to climatic information. In turn it should lead to the evaluation of the temperature niche position of the individual species. Thus, where the variety of fossil species of isotopically unaltered carbonate can be obtained in assemblage form, and provided that these do not constitute a condensation product of skeletal accumulations across a significant climatic gradient or period of fluctua-

tion, reliable information with reference to the various aspects of application considered potentially feasible, heretofore, should be obtainable.

The question whether fossil skeletal carbonates with original isotopic abundances extend back in the sedimentary records in time has been answered in the affirmative for individual cases as far back as the early Jurassic (Urey *et al.*, 1951). Criteria to recognize original O^{18}/O^{16} ratios in fossil carbonate skeletals have been based on the following considerations:

(1) The isotopic ratio-inferred-temperatures lie within a reasonable range of present-day temperatures, e.g. from 0 to 30°C.

(2) Where cross-sectional temperature determinations could be carried out, variations (if they occurred) would follow the familiar pattern of seasonal variations established in present-day carbonate skeletons and lie within a reasonable range.

(3) The inferences from the burial assemblages and their faunal compositional makeup and regional paleogeographic considerations indicate the probability that we are dealing with essentially normal salinity ranges; hence, that the isotopic abundances had not been affected critically by lighter fractions from fresh water dilution or by heavier fractions due to excess insolation, i.e. hypersaline enrichment.

Within the framework of the orientation required from the study of present day biota as to the mode of reliable information, investigations and the criteria employed to evaluate isotopic abundances as to their state of retention of the original composition, Pleistocene (Emiliani and Epstein, 1953; Epstein and Lowenstam, 1953), Tertiary (Emiliani, 1954), and Cretaceous fossils (Lowenstam and Epstein, 1954) have been examined in numbers as far back as the post-Aptian. The most extensive exploratory studies to date (concerned with the potential applicability of the method to the fossil record) were those of mid-to-late Cretaceous assemblages (Urey *et al.*, 1951; Lowenstam and Epstein, 1954). As these are also the oldest assemblages investigated in space and time, the results from the latter study serve best to illustrate the status of information obtained with reference to the various questions raised earlier in this still exploratory phase of the investigation.

The preservation of entirely aragonitic skeletons and aragonitic

micro-architectural units in other skeletons in the Coon Creek fauna at the type locality in Tennessee widened the range of investigation to all burial associated elements. Hence, it has been possible here to integrate average skeletal growth-temperatures of extinct species, to define the approximate amplitude of local temperature variations, and to study the growth ranges of each species within the range as indicated by their average skeletal temperature records. The mean temperature of seventeen species including polychaete annelids, pelecypods, gastropods, and scaphopods extends from 20-28°C, a range of 8°C, which roughly corresponds to that of the Bermuda niche temperatures of today. The average temperatures are reasonable throughout, compared with the present day range and, further, show differences between the gastropods and pelecypods as noted in the Recent Bermuda assemblages. Extended in time to other burial associated species, and supplemented by individual seasonal variation studies, it should be possible to gain in this (as well as similar preservational cases) insight into the climatic framework and the skeletal temperature niches of the biota.

The incidence in preservation of aragonitic skeletal materials has been shown to decrease the further back we go in time in the sedimentary record. Cast and mold preservation, recrystallization or replacement by calcite are numerically vastly more common in Upper Cretaceous deposits than aragonitic preservation. The selective screening processes of aragonitic skeletal material in the common facies range found in the Upper Cretaceous, such as the characteristic chalks, reduces the range of the analysis to the calcitic fraction of the burial records, e.g. to the calcitic skeleton or the calcitic portions where both polymorphs were involved. Ostreidae constitute one of the common calcitic elements encountered in many facies. Loosely meshed layers characterize the shell of many Ostreidae. Infiltration by diagenetically introduced calcite of habitat-foreign isotopic abundances is commonly found in these cases. Hence, calcitic preservation does not *a priori* assure reliable temperature information. This, in turn, further reduces the number of potentially available fossil elements in the aragonite screened facies. Because these facies types form the average situation available for temperature investigations, the analysis became centered on the question as to the extent to which environ-

mental temperature ranges can be determined in these cases, which in turn determines whether species-characteristic temperature threshold limits of their skeletal deposition can be defined.

The common calcitic fossils in this facies range, from sandy marls through pure chalks to coarse bioclastic debris sands, consist of belemnite guards, the prismatic layers of *Inoceramus* species, Ostreidae and brachiopods. Of these, the belemnite rostra had been found early in the investigation (Urey *et al.*, 1951) from several seasonal variation studies and average temperature determinations, to preserve, commonly, original isotopic abundances. Confirmed by subsequent investigations of large numbers (Lowenstam and Epstein, 1954), belemnites were selected as points of reference for evaluation of the isotopic abundances of representatives of other common burial associates. Comparison of such assemblages in limited stratigraphic sequences in individual quarry sections, between quarry sections and also over wide areas, as e.g. from southwest Sweden to the Paris basin, and in time from the Albian through the Maestrichtian, showed the mean temperatures of the few brachiopods examined were consistently higher than those of the associated belemnites, the average difference of 7 brachiopods amounting to about 5°C. In the case of the Inoceramidae there were indications that the average temperatures roughly correspond to those of the belemnites, while those of the Ostreidae appeared to be again elevated (Lowenstam and Epstein, 1954). Poor correlation between belemnites and burial associated Inoceramidae, and randomness with reference to the Ostreidae, and the occasional find of shells with inferred temperatures in excess of 30°C in both groups indicated that secondary calcite introduction has induced shifts in many cases to varying extent, requiring a higher degree of critical examination as compared to the brachiopods. Of the less common burial-associated elements with reliably appearing temperature records, including some aragonitic forms, there are some indications that *Dentalium* representatives have a lower average temperature range; Pectinidae seem to correspond in average temperature to those of the belemnites; and echinoids seem to show a higher temperature roughly corresponding to those of the brachiopods. Numerically, the data in these belemnite associates are few and their skeletal-depositional-threshhold ranges can only be considered as approxi-

mately defined. They seem to corroborate, however, by means of the relations indicated by the brachiopods and the reliable appearing Ostreidae data, that the average temperature of the belemnite lies somewhere in the lower range of the yearly amplitude. Following roughly the time-temperature trend of such benthonic elements as the brachiopods seems to strengthen the view that the nektonic belemnites of the post-Aptian Cretaceous were entirely (or during most of their skeletal growth periods) shelf dwellers. This view is in harmony with the results obtained from functional morphologic studies and their restricted facies distribution.

The results from the average facies faunae though meager as compared to that of the Coon Creek type of assemblage-preservations, nevertheless lead to a number of critical biologic and climatic deductions from the belemnite data. The inference that the belemnites occupied a shelf-water niche rather than migrated seasonally to deeper cooler waters implies that the oscillating curve exhibited by the average temperature data from the post-Aptian through the Maestrichtian depicts the climatic history of this time interval between Scandinavia and the Paris basin. Climatic deterioration from the Albian into the Cenomanian followed by a recurrent rise in temperature to a climatic optimum in the Coniacian-Santonian followed by a decline towards the Danian is thus depicted. The distributional pattern of the warm water *Globotruncana* species follows the same trend in western and central Europe (Wicher, 1953). A slight equatorially northward displaced tropical belt, flanked by relatively cooler boreal zones, though poorly defined, is indicated for the Albian by the belemnite data from widely scattered parts of the world. From southwestern Scandinavia to England and the northern rim of the Paris Basin, essentially uniform climatic conditions are indicated for the Campanian. If a poleward climatic gradient existed it must have been located north of the traverse. Further climatic deterioration in the succeeding Maestrichtian period is evidenced by climatic differentiation along a belemnite temperature traverse from the Gulf coast in the U.S. through Holland northeastward and toward Scandinavia. The indications of similar to perhaps still cooler temperatures for the Danian, as indicated by the few echinoid and brachiopod temperature data in

agreement with the type of Coccolithophoridae found in Danian deposits of Denmark (Henning, 1899), and foraminiferal evidence, accentuates rather than contributes toward solving the problem of mass extinction among marine and terrestrial groups at this time.

Another aspect, to which the paleotemperature determinations do seem to contribute, is an ecologic facet of the belemnites, the evolution of temperature niche occupation. The cosmopolitan distribution pattern of the early Cretaceous belemnites, particularly notable for the Albian species, underwent a sudden restriction in that their descendents become confined to the boreal zones. At first eurythermal, as indicated by the mean temperatures of the Albian species, the belemnites became subsequently stenothermal with temperature tolerance limits ranging from temperate to marginal subtropical. This view is supported by the northward migration of their spacially-defined distribution-zone (from Turonian to early Campanian) in the northern hemisphere reaching into the arctic and shifting subsequently back towards the south thus corresponding to the gross climatic fluctuations indicated. Parallel migratory shifts of the *Belemnitella-Belemnella* species during the Maestrichtian, as shown by Jeletzky (1951), suggest further partition in temperature range on the generic level.

The fairly smooth curve of Upper Cretaceous belemnite data seems to speak against major evolutionary changes in temperature threshhold ranges of the belemnites. The only detailed section at Balswick, Sweden, where temperature data on two genera *(Actinocamax* and *Belemnitella)* in close stratigraphic succession were determined, lacks corresponding evidence of a shift in genus determined threshold limits.

Though still in the exploratory phase of the investigation, the manifold potential contributions by the oxygen isotope method are already in evidence. They pertain basically toward gaining a clearer concept of the threshold limits of skeletal deposition with reference to environmental temperatures in the Recent as well as fossil forms, and toward quantification of the climatic history. It is also evident that evaluation of, and full advantage of the resulting information from, the fossil record is dependent upon the integrated analysis of functional, morphologic, zoogeo-

graphic and paleo-geographic information derived by already established conventional methods.

SKELETAL MINERALOGY

The crystalline calcium carbonate skeletal hard parts of recent marine organisms consist in most cases examined of the two polymorphs calcite and aragonite. Consideration in the following is confined to their distribution relations in marine organisms.

Determinations initially directed towards surveying skeletal polymorph composition in different species were concerned principally with the elucidation of their distributional pattern across the spectral range of carbonate synthesis. Data were accumulated gradually on numerous species in the different phyla. These indicated that single polymorph composition, that is, either calcite or aragonite, was dominant. When viewed in the order of successive levels of increasing complexity in organization, the impression of a random distribution pattern in synthesis products seemed indicated. Polymorph compositions were found largely to be constant on the order level and in the Echinodermata even on the phylum level. By contrast, considerable complexity in polymorphic differentiation on the genus or even in a few cases on the species level was found to exist in the pelecypods and gastropods. In these (comparatively) most thoroughly investigated groups (Bøggild, 1930), coexistence of calcite and aragonite was shown to occur. The determinations of skeletal polymorphs were generally presented without accompanying information on the number of individuals per species examined, their location of derivation or their ecology. The investigations once made were treated as diagnostic for the species and where the composition was found to coincide in several unrelated species, the diagnosis was extended to be inclusive for higher taxonomic categories. The basic assumption underlying such treatment seems to have been that polymorph composition is invariably genetically fixed within a given species or complex of species.

In paleobiologic terms the polymorph composition furnished independent criteria for defining species or higher taxonomic categories. In turn, it extended the potential basis of phylogenetic studies of carbonate skeletons from pure morphologic to crystal compositional aspects. In this, it opened a distinct avenue of

approach to the charting of certain physiologically determined surface expressions of biochemical evolution.

Data accumulating on the polymorph composition and their micro-architectural characteristic in calcareous fossil skeletons soon pointed to the existence of such shifts and occasional compositional changes within a number of phyletic lines. Critical data and the pertinent literature will be found in Bøggild's 1930 study on the micro-architecture and polymorph composition of the Mollusca; it contains notes also on representatives of most major carbonate-secreting groups. Polymorph compositional changes were shown to occur in a number of mollusk lineages and a shift from calcite in the Paleozoic corals to aragonite (with some exceptions) in the post-Paleozoic ones was inferred on grounds of micro-architectural retention in many of the calcite preserved Paleozoic forms. While these examples furnished evidence of factual changes of polymorph composition in certain lineages, and provided indirect evidence for others, the implication that these constitute physiologically determined evolutionary changes was dependent upon the correctness of the basic premise that the polymorph composition in species is generally fixed genetically.

Recent studies have shown, however, that species defined constancy in skeletal polymorphs, while common and perhaps even prevalent among marine carbonate-secreting species is by no means the general rule. Instead, examples have been detected among the Bryozoa, polychaete annelids, pelecypods and gastropods in which the skeletal polymorph compositions vary in species defined terms in individuals as a function of relative age and in response to environmental factors (Lowenstam, 1954 a, b). The range of total variability observed extends from 100 per cent calcite through intermediate mixtures of calcite and aragonite all the way to 100 per cent aragonite. Where examined specifically, the co-existing polymorphs always form micro-architecturally distinct skeletal elements. Also, as far as determined to date, the variability ranges extend for individual species only over parts of the total range of from 100 per cent calcite to 100 per cent aragonite. The general tendency of an increase of aragonite over calcite with increasing environmental temperatures indicates that temperature effect is primarily involved. Two distinct types of relations between polymorph composition and tempera-

ture have been noted: (1) The crystal chemical composition in a given species varies between individuals in response to environmental temperatures over the entire species-defined climatic range. The average polymorph composition of an individual is then dependent further upon an array of factors such as the secretionary range as defined by species characteristic threshold limits, which may or may not coincide with the yearly amplitude of environmental temperatures. It further depends upon the volume secretion of the two polymorphs at a given temperature, again as

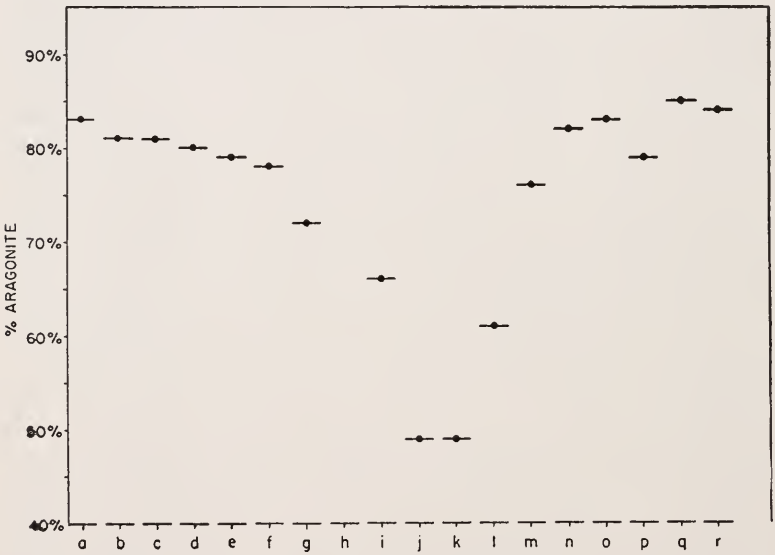

Fig. 1. Variations of aragonite with consecutive growth increments of a recent polychaete worm tube of *Eupomatus gracilis* from Bermuda.

characteristic for a given species, the relative age of the individual, and individual growth rates. (2) The polymorph composition varies only at locations at the fringe of climatic tolerance, but is constant for the species within its climatic range. The temperature-skeletal-polymorph-relations exhibited in the latter type are transitional between species with skeletal-polymorph-deposition independent of the environmental framework and those of the first type dependent throughout. The relation most clearly

defined in the latter type hence will be considered first. The most convincing evidence that a temperature effect is involved should be provided by skeletons in which deposition is confined to peripheral growth expansion. Consecutive growth increment should then consist of polymorph compositions differing as a function of the temperature at which they were laid down. Such skeletons grown in an environment with a large yearly amplitude in temperatures should then exhibit corresponding seasonal variations in polymorph composition. Corroborating evidence is provided by the polymorph compositional changes of successive increments determined for a polychaete serpulid worm tube from the Bermuda inshore waters (Fig. 1). The oscillating curve of the aragonite-calcite ratios is based on the averages of successive cuts of three mm. in length each separated by a gap amounting to 1 mm. The curve defines partially two maxima and one aragonite ratio minimum. The aragonite ratios defining the last growth stages decrease progressively to a minimum. The value of the very last growth portion is slightly lower than the one defining the maximum aragonite ratio peak of an earlier growth stage. The specimen was collected alive on July 2, 1953, at a temperature of 27°C, which is 3°C lower than the summer maximum of 30°C at this location. Hence, the oscillating curve can be interpreted as a seasonal variation curve of temperature-related aragonite ratios. In mollusk shells such as pelecypods, skeleton secretion has been shown to take place not only at the shell margins, but also intermittently on the inside. This obviously negates seasonal variation studies similar to those feasible for serpulid worm tubes. A measure of the existence of a temperature effect on the shell polymorphs can be obtained, however, even here by determining the aragonite ratios of graded shell size series representatives of the size range of habitat-associated conspecific populations. This has been demonstrated, e.g., in a growth series of *Mytilus californianus* (Lowenstam, 1954 b) (Fig. 2) where the oscillating curves thus obtained showed correspondence to a 2 year period, with the largest shell corresponding to a 2 year old individual as determined by the growth studies of Coe and Fox (1942). Obviously the aragonite ratios of the individual shells represent averages of the growth period. Hence, the aragonite-calcite minima and maxima ratios defined by the oscillation

curves thus obtained in pelecypods and gastropods do not correspond to the values of secretion at the opposite ends of the yearly temperature range as in the growth increments in the Serpulidae tube.

The secretionary behavior pattern of skeletal polymorphs of the second type is illustrated by the subtropical to tropical gastropod species *Littorina ziczac*. Individuals analyzed from Bermuda and the Keys of Florida showed shell compositions of 100 per cent aragonite throughout, while those taken from the marginal

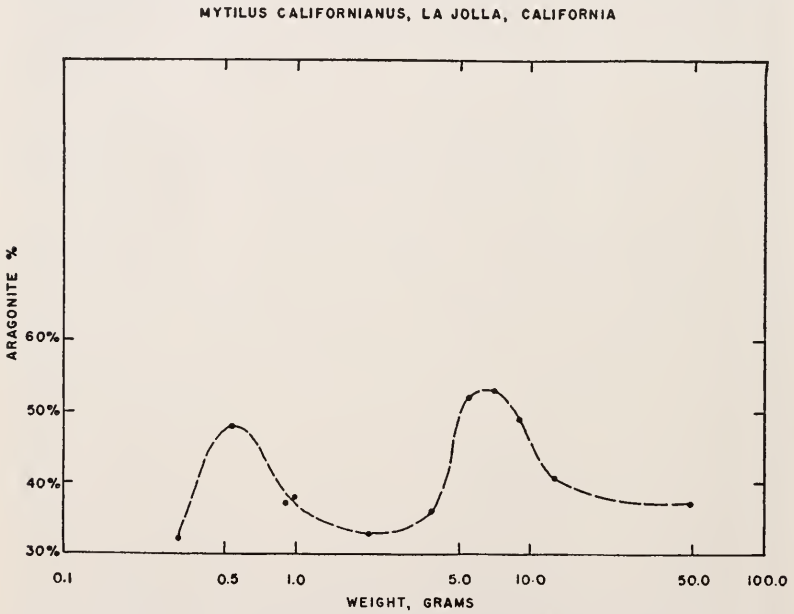

Fig. 2. A plot of shell weight of *Mytilus californianus* versus aragonite in the shells taken from a single growth series from La Jolla, California.

temperature range at Galveston, Texas, where temperatures extend down to 14.3°C exhibit traces of calcite as indicated by the range from 97 per cent aragonite to 100 per cent aragonite. A skeletally defined temperature effect in the polymorph composition here as in other species reported (Lowenstam, 1954) is thus clearly confined here to the marginal climatic range.

The relations to temperature indicated by the skeletal-poly-

morph composition in species of the two types are consistent in that they conform to a common pattern of increase in aragonite over calcite with elevation and temperature. The relations differ in that the polymorph ratios in species group 1 may increase only to very high aragonite values without total suppression of the calcite fraction, while in species in group 2, threshhold conditions for 100 per cent aragonite synthesis are attained commonly in the range from warm temperate to marginal subtropical temperatures. There is secretion of aragonite only from there on up through the subtropical to tropical temperatures, which define most of the entire range of species in this group. This raises the question whether constant polymorph composition as found in many species can be considered *a priori* as a sound criterion of species-determined-modification-synthesis, independent of ecologic controls such as temperature. There are numerous species with constant aragonite-composed skeletons which are distributionally confined to warm water temperature range. For instance, in the genus *Choromytilus*, the tropical species *palliopunctatus* has, where examined, a shell composed of 100 per cent aragonite. If the species were capable of occupying colder-water niches, threshold conditions for calcite secretion would likely be attained with the result of shifting aragonite-calcite-ratio of secretion similarly to that actually found in the cooler-water niche occupants (the species *meridionalis* and *chorus* of this genus). Corroboration of the interpretation that a temperature effect is the determining factor in the constant aragonite composition of the tropical species seems here to be provided by examining jointly the modification synthesis pattern of congeneric species occupying successively higher temperature niches as similarly observed, e.g. in the Littorinidae and Spirorbinae (Lowenstam, 1954 a, b). Based on these observations the interpretation of temperature-determined-modification-synthesis has been extended to embrace species with constant aragonitic skeletons over their distributional range in which all species in a given genus, order or even class are either confined to the warm water range or only there synthesize aragonite or skeletal carbonate as such. This is the case in the green, brown, and red aragonite secreting algae, the aragonite secreting alcyonarians and numerous pelecypod and gastropod species such as the Tridacnidae and Cypraeidae. The abrupt

reduction in number of species of scleractinian corals, aragonitic in skeletal composition throughout at the lower subtropical temperature limit from the wealth of reef building forms above to a few deep water type species below, then seems to be the least conspicuous expression of the grading spectrum of temperature related polymorph compositional patterns so far noted.

At this early phase of the inquiry, temperature affected modification synthesis has been widely recognized to extend over the phyla spectrum of increasing complexity discontinuously from the Anthozoa to the Mollusca and to the calcareous algae. Species with temperature-sensitive aragonite-calcite ratios are found among the Bryozoa, polychaete worms, gastropods and pelecypods, while those with constant aragonite composition throughout are confined to the warm water range among the Anthozoa, gastropods, pelecypods, and polychaete worms.

In relating temperature as a determinant on the calcite or aragonite secretions or both in varying ratios, it is not known at present whether temperature acts directly upon the biochemistry of the secretionary processes (i.e., determines certain enzyme activation between certain threshold temperatures and the activity levels over their defining ranges) or, whether temperature affects intermediate steps in the reaction, such as an effect by temperature of external environmental properties such as the pH of the surrounding aqueous mediums which in turn effects the biochemistry of the secretionary processes. Differences in the aragonite ratios and the range in value as found among species occupying the same habitat, and hence subject to the same yearly amplitude in environment, demonstrate, however, that species-determined differences in biochemical reactions (of whatever nature they may be), are involved. Some of the differences in range of variations in aragonite ratios may be attributed to species determined differences in threshold limits of carbonate secretion. This aspect has been brought into focus and furthermore demonstrated in an example among pelecypods in the discussion concerning oxygen-isotope-determined-shell-growth-temperatures. Other species-determined-modifying-effects possibly concerned, suggested by Epstein and Lowenstam (1953), may involve differences in volume secretion of the aragonite calcite ratios at a given temperature and in some cases intermittent

partial skeletal resorption.

Other environmental factors may also affect, though to a lesser extent, the aragonite calcite secretion (Lowenstam, 1954 a, b). At present the possibility of a salinity effect seems indicated. The aragonite-calcite ratios in species occupying brackish waters appear to be considerably higher in conspecific populations than would be expected for the species within the temperature range which they occupy.

In the Littorinidae some species with entirely aragonitic shells may be found in temperate climates side by side with species with temperature affected shifting aragonite calcite ratios. Ecologically, it can be shown that the former species is more advanced in its adaptation to subaerial respiration and is interpreted as physiologically more independent of temperatures because of its higher degree of adaptation to land life, as compared with the latter.

The implications discernible at this stage of the investigation of recent forms concern primarily the definition of species with temperature affected polymorph composition other than those where the polymorph composition is constant throughout. In terms of the two parameters: temperatures and aragonite-calcite ratios and their range involved, *Littorina ziczac* can be defined as 97-100 per cent aragonite/14°-30.5°C. As shown by numerous investigators most admirably by Bøggild (1930) in the Mollusca, the two polymorphs, where they are found coexistent in the shell of a given species, form micro-architecturally separate elements. These are found in layered succession or sometimes alternation and differ microstructurally not only between polymorph-defined layers but may be differentiated further in the layered succession in monomorphic units. One of the obvious questions since raised by the discovery of a temperature effect on skeletal polymorph composition concerns the micro-architectural changes involved in the change from aragonite and calcite bearing shells to entirely aragonitic ones. In the Mytilidae, in the species *californianus* from La Jolla, the outer calcitic portion is composed of a prismatic layer of, in part, regularly vertically arranged, and in part slightly inclined, crystals similar to that found in the species *edulis*. The aragonitic portion of the shell consists of the common nacreous type distinguished by Bøggild, which forms thin-leaved

lamellae essentially parallel to the shell curvature in *edulis*. In the species *perna* shells from Manila, Philippines, and the South China Sea with entirely aragonite exoskeleton show two nacreous units in succession. The outer aragonitic unit consists of lamellae which are steeply outwardly inclined, then curve downward to become parallel to the shell axis and thus acquire here the structural attitude of the lower aragonitic unit steeply outwardly inclined but curved downward. The outer lamellar aragonitic layer corresponds to the prismatic calcitic layer in the species *californianus* and *edulis*. Hence, in an extreme shift such as the one discussed from a shell composition of coexistent aragonite-calcite to 100 per cent aragonite, the ecologic, that is the temperature, effect involves further a radical change in micro-architecture, perhaps basically determined by crystal chemical growth characteristics.

The development of trace amounts of calcite only in the marginal temperature range of otherwise aragonite-secreting species may find application in paleoecologic research. The lower limits of the climatic range, hence the evaluation of the geographic range, may be thus detectable in similar fossil occurrences.

The most critical implication, however, concerns the realization that polymorph compositional and related micro-architectural changes in species traced back in lineages through geologic times are not necessarily to be attributed to evolutionary changes but may be purely ecologic expressions. The supposed mytilid *Cuneolis tippana* from the Maestrichtian Coon Creek deposits of western Tennessee composed entirely of aragonite is a case in point. Polymorph shell composition at variance with that of *Mytilus edulis* (Bøggild, 1930; Stephenson, 1941) which was until recently thought to be representative of the Mytilidae lineage, had been considered of evolutionary significance. As noted in the discussion of the paleotemperature determinations of parts of the Coon Creek burial assemblages, the environmental water temperatures were shown to be subtropical. The average shell-determined temperature of *Cuneolis tippana,* one of the species analyzed by the oxygen isotope method, assures further its derivation from this climatic niche. Lying within the temperature range where present, Mytilidae secrete entirely aragonitic shells; the same shell composition in *Cuneolis tippana* can be attributed to

its ecologic temperature niche rather than an evolutionary change.

Aside from *Cuncolis tippana,* Bøggild (1930) called attention to differences in crystal polymorph composition between present-day and fossil representatives mostly in other families of the pelecypods, gastropods, cephalopods and the Anthozoa but without interpreting their biologic significance. The differences are in part factual, that is they are based on observed differentiations in crystal polymorph compositions. In part they are inferred, based on the evaluation of calcite-preserved fossils as to whether their skeletal calcites are primarily secretionary in origin or conversion or replacement products of original aragonite. Crystal arrangement and orientation in their relations to micro-architectural preservation constitute Bøggild's criteria for differentiating the two. Differences in crystal polymorph composition between fossil and present-day representatives, based on the latter criteria, are therefore interpretive in nature and their reality is dependent upon the validity of the criteria employed. In the pre-Cretaceous deposits aragonite preservation in skeletal carbonates is, as earlier pointed out, rare; hence tracing of the polymorph compositional characteristics here becomes largely interpretive. Therefore, when considered in conjunction with the as yet inadequate information on crystal polymorph distribution in present day biota, which initially constitutes our plane of reference for comparison, the inquiry into aspects of skeletal evolution is best confined at this stage toward interpretation of the published data in phyletic lines and largely as a matter of orientation. Crystal polymorph compositional determinations of fossils exist only for a few time-distant representations of the various lineages in which compositional changes were reported by Bøggild. The patterns derived from these, if they indicated trends in polymorph compositional changes in consequence must be treated with utmost caution as to their evolutionary implications and can at best be regarded as probable rather than certain. From the methodical point of view, examples with the least complex relations are the most desirable for the initial analyses. Therefore, consideration of those groups in which present-day species indicate either throughout or at most a partial temperature effect on their skeletal-crystal-polymorph compositions, seems best postponed at least until the relations for all present-

day species have been precisely defined. This eliminates most pelecypod and gastropod lineages in which polymorph composition changes were indicated by Bøggild. This view is fully justified in the light of the earlier noted example of *Cuneolis tippana* which in consequence of the relatively more representative data

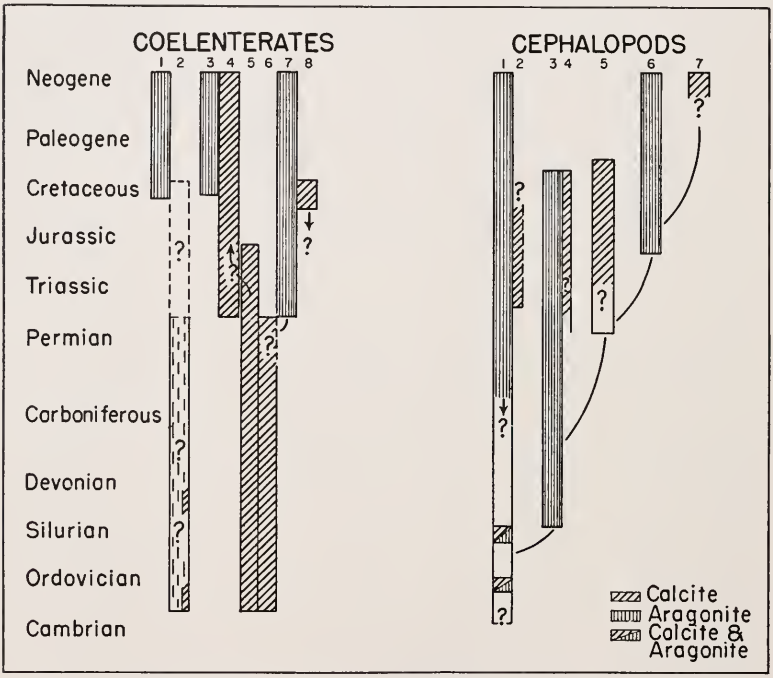

Fig. 3. A schematic presentation of some inferred phylogenetic changes in crystal polymorph compositions. (Fossil data from Bøggild.) Coelenterates: 1. Hydrocorallina, 2. Stromotoporoidea, 3-4. Alcyonaria, 5. Tabulata, 6. Rugosa, 7-8. Scleractinia. Cephalopods: 1-2. Nautiloidea, 1. shell, 2. beak tippings; 3-4. Ammonoidea, 3. shell, 4. aptichi; 5. Belemnoidea; 6. Sepioidea; 7. Octopoda.

for the present day Mytilidae could be evaluated to the effect that the aragonitic shell can be related to environmental control and not to an evolutionary change.

Groups which comprise species with single crystal polymorph composition which are today either environment independent

throughout, or where the type of polymorph secretion seems to be temperature determined but remains unchanged over the niche range of the species, would seem best suited for the analyses of few time-distant representatives with crystal polymorph determinations in phyletic lines.

Changes in crystal polymorph composition in the course of evolution of groups of this type have been reported by Bøggild for the Coelenterata and Cephalopoda. Their crystal-polymorph-compositional-distribution relations as derived from Bøggild's data are schematically shown in Figure 3. The principal features of the relations indicated are: 1) the skeletal-polymorph composition of the fossil representatives indicated at variance with those of the present-day species, appear so far as determined, prevalently monomorphic in most cases for all members of a given family, order, or even subclass, which is analogous to the present day representatives. 2) Once a compositional change became initiated, the composition appears to have remained constant from the start of differentiation of the group, as far as determined, until the present day or until extinction. 3) The changes in polymorph composition in the cephalopods coincided and were apparently related to effects which involved profound changes in morphology and body function of the skeletal hard parts in conjunction with anatomical reorganization that determined their relocation in the body. 4) "Organo-typic" that is, anatomically localized calcium carbonate secretion, occurred in the course of evolutionary phases in the cephalopods. These are the calcitic aptychi in the Mesozoic ammonites and beak calcitic calcification in the nautiloids. In all cases these differed in their calcitic compositions from that of aragonitic shells. 5) Calcite appears to have formed the secretionary product more prevalently in the early phases either alone as in many Paleozoic coelenterate groups, or was coexistent with aragonite in the early nautiloids. Aragonite seems to have become more prevalent in the later phases in evolution in these cases either through group replacement with aragonitic skeletal bearing types, as indicated by the change from calcite in the Paleozoic tetracorals to the aragonitic scleractinians, or, as in the alcyonarians, it occurred through late introduction of aragonite secreting groups. Thus if any reliance can be placed on the crystal polymorphs assigned to the earlier

representatives on grounds pointed out previously a slight net gain in spread of aragonite over calcite seems to be indicated. More reliable data based on added criteria of evaluation of calcitic skeletons in the lower half of the stratigraphic column are obviously required to ascertain whether the indicated relations are correct.

TRACE ELEMENT CONCENTRATIONS

The trace element content of skeletal carbonates has long been the subject of investigation. For most elements the widely scattered literature[1] shows that the studies have been limited in scope and confined to small biotic groups or to scattered individual analyses. Two major trace elements, strontium and magnesium, are notable exceptions. In recent years broad surveys of the distributional abundances of these elements have been made with improved techniques over the range of the phyla spectrum of carbonate synthesis. The biogeochemistry of strontium has been investigated by Odum. To date only the general conclusions and certain phases of the study have been published (1950-51). Magnesium has been studied, principally in the calcite-secreting biotic representatives, by Chave (1954). The toleration of strontium is greater in aragonite than in calcite while magnesium is more acceptable in calcite than in aragonite.

The two studies clearly establish the significance of skeleton trace element chemistry as an added source of information on physiologic, and therefore phyletic aspects. There are certain common features that determine the distribution levels of both elements. Within the limits imposed by the toleration of the crystal chemical composition the physiology of the species as determined by its phyletic position controls the uptake ranges of these groups. The strontium uptake is apparently ecologically dependent only on the concentration in the aqueous medium. In the case of magnesium, temperature plays a major role.

The initial discovery of a temperature effect on the magnesium

[1] The widely scattered information on the biochemistry of marine organisms has been brought together and interpreted by Vinogradov. Thanks to G. E. Hutchinson this work has been translated into English, brought up to date and the bibliographic presentation revised to allow easy consultation of references cited in the text.

level in certain biotic groups was made by Clarke and Wheeler (1922). The work of Chave (1954) has shown that a temperature effect is generally involved in calcite-bearing species throughout the entire phyla spectrum. He shows that the effect may further extend to the low magnesium types of aragonitic skeletons. Attempts to quantitatively evaluate the temperature effect can now be made. Certain deviations from the trends in the temperature-magnesium concentration relations are interpreted to denote discontinuous skeletal growth. This is consistent with relations shown to exist by the oxygen isotope method (Urey *et al.*, 1951; Epstein and Lowenstam, 1953).

The concentration relations of magnesium exhibited by the calcitic skeletal types may provide another independent index of the temperature. They are subject, however, to modification by physiological influences reflecting the phyletic position these occupy.

The isolation of environmental effects such as temperature on the magnesium levels is dependent upon selection of appropriate specimens where environmental data pertinent to the evaluation are available. The same approach has brought out the existence of the earlier noted temperature effects on the polymorph composition as expressed in aragonite ratios. Although temperature has no apparent influence on the strontium levels in either calcite or aragonite, the temperature influence on the crystal polymorph ratios should be reflected in the total strontium content of the calcium carbonate skeleton. In consequence of the increase in aragonite content with elevation in temperature, it would follow that the strontium concentrations for the skeletons as a whole should increase with the elevation in temperature. This has been demonstrated in the case of the serpulid worm tubes where there is a trend of increasing strontium concentration between the calcitic cold water and nearly all the aragonitic warm water end members of a series examined (Lowenstam, 1954a).[1] The same relations have since been noted in two small population samples of *Littorina littorea* from the Mt. Desert area in Maine with the magnesium, barium and manganese levels paralleling the trend, though differing in particulars. These examples indicate then

[1] These, as well as all subsequent trace element data discussed were determined spectrographically by O. Joensuu of the University of Chicago.

that temperature may indirectly, through its effect on the aragonite ratios in certain species, also control the total strontium concentrations of carbonate skeletons. It should be noted, however, that the data for the Mytilidae are as yet inconclusive and those for the Littorinidae as a whole seem to be so far negative. Other local ecologic factors appear to be involved in the latter case. Therefore, not until the same relations observed in the Serpulidae and local *Littorina* populations have been established in other biotic groups with temperature-sensitive-skeletal polymorph-compositions would it seem legitimate to assume that we are dealing with a widespread phenomenon. Despite this distributional uncertainty, the fact that temperature may indirectly affect, via the shifting aragonite-calcite ratios, total strontium levels in skeletal carbonates at all, adds basically another ecologic factor to the one pointed out by Odum (1950). With regard to the influence of the aqueous medium on the strontium concentration, it is worth noting that biotic mass fixation of high strontium bearing aragonites, by green, red, and brown algae, scleractinian corals, and serpulid worms on the warm water reef sites may in turn affect the concentration levels locally in the waters. Strontium fixation is here faster than the rate of mixing (Lowenstam, 1954b). This is at least indicated by a comparison of the strontium-calcium ratio of four water samples from over two reefs, which on the average are lower by about 15 per cent as compared with that of six samples from cold to temperate waters. Spirally directed water circulation as shown for Bikini and Bermuda (Boden, 1952), restricted by the biochemically active reef front, would seem a plausible mechanism to explain the biologic effect on the strontium-calcium ratios of the waters here. Verification by additional data is clearly needed before its implications can be projected into paleobiologic consideration.

Regarding the paleobiologic aspects, Odum (1951) and Kulp *et al.* (1952), have examined the distributional aspects of strontium in fossil carbonates. Where original carbonate compositions are preserved, as is commonly the case through the Tertiary but rarely through the Paleozoic, the results are encouraging. In general, however, conversion, or replacement following solution-removal of aragonite, is accompanied by reduction in strontium levels. Older samples tend to have the biologic abundance levels

modified. Chave's study on magnesium distribution in fossils is still to be published.

The present task in the trace element studies is the elaboration of the principles governing the relations under investigation as found in present-day biota. It is further dependent upon the understanding of the post-mortem geochemical processes imposed upon the skeletal remains of the fossil records.

The foregoing discussion of the present status of investigations of the various biogeochemical aspects of skeletal building materials, viewed in this case for that of calcium carbonate, shows that at this early phase of the inquiry primary concern rests with the elucidation of relations in present day biota and the formulation of the principles involved. The application to the paleobiologic inquiry pertains as far as discernible at present to: (1) added criteria of taxonomic groups in physiologically determined crystal chemical and trace element concentration expressions; (2) qualitative and quantitative evaluation of ecologic factors such as temperature through the O^{18}/O^{16} ratios through skeletal carbonate secretion in polymorph compositional terms and their trace element concentration levels; (3) the charting of phylogenetic changes in the area of biochemical evolution as reflected in skeletally preserved expressions and in ecologic, e.g. temperature-defined, niche tolerances.

In the area of actual application, only the paleotemperature method which utilizes the O^{18}/O^{16} ratios has been extended to fossil investigations systematically, as shown by its successful application as far back as the Liassic, and in regional terms to the post-Aptian Cretaceous, where the results are most encouraging. These pertain to a better evaluation of the biology of the belemnites and their temperature niche adaptational evolution from mid- to late Cretaceous time, and to the semi-quantitative evaluation of the climatic history of this time interval. The results corroborate the qualitative temperature evaluation obtained earlier from zoogeographic studies for this time interval. These underline the thesis that the value and the rate of progress in the area of concern by any of the biogeochemical studies is dependent upon an integration of the various approaches rather than separate operation in a vacuum.

Because of the preoccupation with defining the basic relations

as observable in present day biota, the applications of the polymorph compositional relations and trace element abundances are as yet few or, in the case of evolutionary trends, suggestive rather than proven. In principle these approaches have basically contributed in orienting the inquiry into paleoecology and skeletal evolution, and in their various degrees of proven application have extended the foundations of inquiry into these aspects.

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Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 112, No. 4

REVISION OF THE CHRYSOMELID SUBFAMILY AULACOSCELINAE

By F. Monrós

Fundación Miguel Lillo, Tucumán, Argentina

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PRINTED FOR THE MUSEUM

November, 1954

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 112.

Breviora (octavo) 1952 — No. 35 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 33 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 17 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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No. 4 — *Revision of the Chrysomelid Subfamily Aulacoscelinae*

By F. Monrós

INTRODUCTION

Since Crowson's revision of *Aulacoscelis* in 1946, several changes have been introduced in the group, so that it seems time to study it again.

I have undertaken the present revision because I have been able to examine all the described species (76% of them on the basis of type specimens) and also because it seems worth while to make a more detailed study of a group of Chrysomelidae which, from a theoretical point of view, figures among the most interesting of the whole family.

MATERIAL STUDIED AND ACKNOWLEDGEMENTS

An alphabetical list of the collections examined follows, with the abbreviations used in the text and the names of the entomologists who made the examination possible, to all of whom I want to express my best thanks.

California Academy of Sciences, San Francisco (CAS) — Mr. H. B. Leech.

Carnegie Museum, Pittsburgh (CM) — Dr. G. Wallace.

Chicago Museum of Natural History (CMNH) — Mr. R. L. Wenzel.

Cornell University, Ithaca (CU) — Dr. H. Dietrich.

Museum of Comparative Zoology, Cambridge (MCZ) — Dr. P. J. Darlington.

Philadelphia Academy of Sciences (PAS) — Dr. A. G. Rehn.

United States National Museum, Washington (USNM) — Dr. E. Chapin.

Wilcox collection, Albany, N. Y. (W) — Dr. J. C. Wilcox.

I also want to thank the John Simon Guggenheim Memorial Foundation for making it possible to study the chrysomelid collections in the United States, and also to collect in the southwestern states, and to make some observations on living *Aulacoscelis*.

Finally, I want to express my gratitude to the following persons, who contributed in different ways to make the present revision possible:

Dr. W. H. Anderson, U. S. Dept. of Agriculture, Washington, for some specimens of Aulacoscelinae intercepted at the Mexican border.

Dr. E. B. Britton, British Museum of Natural History, London, for sending paratypes of *Aulacoscelis melyroides* Crowson, at my request.

Dr. P. J. Darlington, Cambridge, for kindly reading the manuscript and correcting the language, as well as for the facilities given at all times.

As for the collections in the Museum of Comparative Zoology, the following remark seems necessary : Most of the Aulacoscelinae studied are in the Bowditch collection, which is based mostly on Jacoby's material. Some of the specimens which have been used by Jacoby in the *Biologia Centrali Americana* and are now in the Bowditch collection have a "type" label, while specimens of the same species in the British Museum also studied by Jacoby have been regarded as "types" by Crowson. As it seems difficult and almost useless to establish which of these specimens must be considered as the holotypes, I regard all the specimens used in the *Biologia Centrali Americana* which fit Jacoby's original descriptions and localities as cotypes, regardless of the collection in which they are now deposited.

HISTORY

1842. Duponchel and Chevrolat briefly described the genus *Aulacoscelis* and the species *melanocera* which they considered close to *Phyllocara* (Chrysomelinae). The genus and species were credited to Chevrolat in Dejean's catalogue, 1837, but the reference cannot be taken into account, as in that catalogue both terms are *nomina nuda.*

1865. Without referring to the previous description by Duponchel and Chevrolat, Stål described *Aulacoscelis melanocera* which he placed among the Chrysomelinae, without analyzing its relationship.

1874. Chapuis created the tribe Aulacoscelini (Aulacoscélites in Chapuis), and transferred the genus *Aulacoscelis* from the Chrysomelinae to the Sagrinae; he described a second species from Guatemala.

1874. Gemminger and Harold listed the known species of *Aulacoscelis* as Sagrinae.

1877, 1880 and 1888. Jacoby described and illustrated several species and listed the *Aulacoscelis* known to occur in Central America. He placed the genus in the Sagrinae, without further analysis.

1892. Horn described *Aulacoscelis purpurea,* from southwestern United States.

1903. In the revision of the genera of Sagrinae for Wytsman's *Genera Insectorum*, Jacoby excluded *Aulacoscelis* which he referred to the Chrysomelinae.

1913. Clavareau listed the known species of *Aulacoscelis*, numbering 12. He placed the genus in the tribe Aulacoscelini at the end of the Sagrinae.

In the more recent catalogues (Leng, 1920 and supplements; Blackwelder, 1946), *Aulacoscelis* has also been included in the Sagrinae.

1933. Schaeffer described *Aulacoscelis ventralis*, from Arizona.

1941. Maulik briefly stated that *Aulacoscelis* cannot be considered as belonging to the Sagrinae.

1946. Crowson published a careful revision of the genus which he placed in a special tribe in the Sagrinae. It is to be noted that in this paper the Sagrinae had a broad sense, including *Orsodacna* and related genera, now split into as many as three different subfamilies (Orsodacninae, Zeugophorinae and Synetinae), and the tribe Hornibiini, which is now considered to be a tribe of primitive Eumolpinae. In the key to species, Crowson omitted *A. melanocephala* and wrongly credited *A. melanocera* to Jacoby.

1949. Monrós excluded Aulacoscelini from the Sagrinae and suggested a position among the primitive Eumolpinae.

1950. Bechyně described *A. costaricensis*, from Costa Rica.

1953. Monrós described the new genus *Janbechynea* from Bolivia and defined the new subfamily Aulacoscelinae, which he considered close to Chrysomelinae.

PUBLISHED ILLUSTRATIONS AND MORPHOLOGICAL DATA ON AULACOSCELINAE

General habitus illustrations of the following species have been published in color:

Aulacoscelis candezei (Chapuis, 1874, pl. 111, f. 6; Jacoby, 1888, pl. 35, f. 7).
A. confusa (Jacoby, 1888, pl. 35, f. 6).
A. sanguinea (Jacoby, 1888, pl. 35, f. 10).
A. melanocephala (Jacoby, 1880, pl. 1, f. 1).
A. variabilis (Jacoby, 1888, pl. 35, f. 8, 9).
A. tibialis (Jacoby, 1888, pl. 35, f. 2).
A. grandis (Jacoby, 1888, pl. 35, f. 1).
Janbechynea fulvipes (Jacoby, 1888, pl. 35, f. 3, 4).
J. elongata (Jacoby, 1888, pl. 35, f. 5).

The following species have also been illustrated:

Aulacoscelis melanocera (Monrós, 1949, f. 22).
Janbechynea paradoxa (Monrós, 1953, f. 1, 2).

Also the following parts have been described and figured:

Labium and maxilla of *Aulacoscelis candezei* (Chapuis, 1874, pl. 111, f. 6a, 6b); labium of *A. melanocera* (Monrós, 1949, f. 6) and buccal pieces of *Janbechynea paradoxa* (Monrós, 1953, f. 3-6).

Ventral thoracic morphology of *Aulacoscelis högei* (Crowson, 1946, f. 26) and lateral prothoracic of *A. melanocera* (Monrós, 1949, f. 9).

Wing venation of *Aulacoscelis högei* (Crowson, 1946, f. 13), *A. melanocera* (Monrós, 1949, f. 14), and *Janbechynea paradoxa* (Monrós, 1953, f. 8).

Tarsi of *Janbechynea paradoxa* (Monrós, 1953, f. 7).

Metendosternite of *Aulacoscelis högei* (Crowson, 1946, f. 23).

Male genitalia of *Aulacoscelis melanocera* (Monrós, 1949, f. 21).

As can be seen, 70 per cent of all the known forms of the group have been illustrated, which is much more than the average in the Chrysomelidae. The morphology of the Aulacoscelinae is also one of the best known of the entire Chrysomelidae. In spite of these facts, however, their systematic position has been much confused.

CHARACTERS OF SUBFAMILY AULACOSCELINAE

Of elongate and more or less parallel shape; ventrally pubescent. Head not concealed under thorax, pro- or orthognathous. Clypeus separated from interocular space by a distinct transverse depression. Eyes rounded, entire, moderately projecting, not touching anterior margin of prothorax. Antennae inserted on sides of head, between eyes and base of mandibles, separated by entire width of frons and not able to be concealed under ventral surface, subfiliform to slightly serrate, nearly as long as or little longer than one half the body length. Palpi not truncate at apex. Ligula semimembranous and distinctly bilobed. Dorsal surface of head without deep interantennal crossed sulci.

Prothorax narrower than base of elytra, with distinct and entire lateral margins and evident angles, all without sensorial setae. Prosternum narrow but visible between procoxae, the latter projecting and transverse; procoxal cavities closed behind.

Mesosternum advanced between mesocoxae which are moderately separated. Metendosternite as shown in Figure 53.

Elytra longer than abdomen, rather soft and often with carinae or tubercles, slightly to moderately dehiscent at apex and without regular rows of punctures.

Wing venation of the Chrysomelinae-type, without cells between M3 and CuII.

Femora not dilated and without teeth. Tibiae with two small but distinct apical spurs on inner edge. Tarsi without empodium, third segment slightly bilobed ; claws simple, equal and divergent.

Abdomen with five visible sternites, the last with sexual differences.

Male genitalia with tegmen forming a ring prolonged ventrally in a long median process and entire dorsally, and with lateral lobes articulate ; median lobe with two long basal median struts under which the internal sac is protected.

SYSTEMATIC POSITION

The combination of characters just described easily distinguishes the Aulacoscelinae from the remaining Chrysomelidae. It is not easy, however, to establish its relationship, as the group presents a misleading mixture of characters which conceal its real affinities.

The bilobed ligula appears only in the primitive Chrysomelidae as a character which they retain in common with the Cerambycidae. The Aulacoscelinae need thus to be differentiated only from the other Chrysomelidae with bilobed ligula, from all of which they are easily distinguished by the pronotum with entire and distinct lateral margins. From the Bruchidae, also with bilobed ligula and undoubtedly related to the Chrysomelidae, the Aulacoscelinae differ by the non-pedunculate mentum and their entirely different shape, as well as probably a different biology. From the Cerambycidae too, they may be easily distinguished by the cephalic and ocular morphology and antennal insertion, as well as probably by different larval biology.

From the other Chrysomelidae with bilobed ligula, the Aulacoscelinae may be distinguished not only by the prothoracic structure but also in different cases as follows : From the Sagrinae by absence of cephalic sulci, simple hind femora, and tibiae with apical spurs. From the Orsodacninae (including the subfamilies Zeugophorinae and Synetinae, of dubious significance), by the simple claws. From Megalopinae, by the antennal shape, non-constricted sternites, tarsi without empodium.

The only significant character which the Chrysomelidae with bilobed ligula seem to have in common is the bilobed ligula itself, and each of the subfamilies which possesses it seems to represent

a different phylogenetic line, so that they can hardly be grouped together in one section, as is customarily done, under the name of Eupoda. The section Eupoda seems to cut across the true relationships of the chrysomelids, and so appears to be of no use. The term may be retained to designate the group formed by Sagrinae, Donaciinae and Criocerinae, which represent one evolutionary line.

Except for the Hispinae and Cassidinae, of which the connections with the rest of the Chrysomelidae are not yet known and which should perhaps be considered as forming a separate family, comparable in distinctness to the Bruchidae or the Cerambycidae, all the more specialized groups of Chrysomelidae seem to have retained some primitive members represented by the forms with bilobed ligula. Thus, the Sagrinae may be placed at the base of the line leading to the Criocerinae and the Donaciinae; the Megalopinae, at the beginning of the line of *Camptosoma,* in spite of the different larval habits and several other minor differences which make the relationship not very close; *Orsodacna* and allied genera (whether or not they are considered to form different subfamilies and excluding the Zeugophorinae which seem to be no more than a tribe of the Megalopinae) at the beginning of the line of Eumolpinae, and the Aulacoscelinae, at the beginning of the line of the Chrysomelinae and Alticinae-Galerucinae.

This does not mean that the Aulacoscelinae can be considered as direct ancestors of the Chrysomelinae, nor that the center of origin of this section can be placed in Central America, but simply that the tendency which culminates in the more specialized Chrysomelinae or the still more specialized Alticinae-Galerucinae is already present in the Aulacoscelinae. The latter must be considered as a relict and one which may illustrate the probable general appearance of primitive Chrysomelidae.

In connection with that point of view, the genera of the Chrysomelinae need to be rearranged and *Timarcha,* with a male genital structure closely resembling that of the Aulacoscelinae, must be placed at the beginning of the Chrysomelinae; the order of the remaining genera must be reversed so that the more specialized Doryphorini are considered at the end, and not at the beginning of the Chrysomelinae

Each one of the lines analyzed represents a natural unit and

may be identified by a name. The term Cyclica may be applied to the phylogenetic line represented by Aulacoscelinae-Chrysomelinae and Alticinae-Galerucinae, and there seems to be no good reason to subdivide it into Cyclica *s. str.* and Trichostoma as is frequently done.

GEOGRAPHIC DISTRIBUTION
(Figures 2, 3)

The Aulacoscelinae are restricted to the Western Hemisphere. The Central American mainland has most species, and two species of *Janbechynea* are found as far south as Peru and Bolivia; the same genus (subgenus *Bothroscelis*) has extended north to the southwestern United States, where also the genus *Aulacoscelis* is known to occur. The North American specimens of *Aulacoscelinae* are the extreme northern representatives of species which have their center farther south. As for *Aulacoscelis högei,* reported by Jacoby from Vancouver Island in western Canada, it is probably an error of labeling.

The subfamily is absent in the Caribbean Islands and in Florida, in spite of the fact that it is found at equivalent latitudes on the Central American mainland.

BIOLOGY AND ECOLOGY

According to the labels which accompany some of the specimens studied, the host plants of adult Aulacoscelinae are the following:

Aulacoscelis candezei, flowers of Compositae in New Mexico (Monrós).

A. melanocera, Cycas revoluta in Mexico and El Salvador; "Palm" in Honduras (this could also refer to Cycadaceae, commonly known as "sago palms") (Specimens in USNM).

A. costaricensis, leaves of *Cycas revoluta* in Costa Rica (Specimens collected by Nevermann in USNM).

Janbechynea elongata, cycads in Mexico, with the remark "infestation heavy." (Specimens intercepted at Laredo, now in USNM.)

In the United States National Museum collection there are some unidentified specimens of *Aulacoscelis* from the Rio Grande area in southern Texas collected by G. Vogt on flowers of *Hechtea texensis* (Bromeliaceae); their specific identity has not been established.

Nothing is known of the host plants of the remaining species, and no larva has yet been collected.

It is worthy of note that the Aulacoscelinae are absent from Florida and the West Indies, even though *Zamia* and other cycads are known from these areas. In the case of the South American species of *Janbechynea* the host plant association is not established, but the coincidence of their ranges with those of Cycadaceae in South America is perhaps suggestive.

Aulacoscelis seem to prefer semi-arid regions and in spite of some exceptions, for instance *A. costaricensis* and *A. melanocera* found in tropical rain-forest, most of the species occur where semi-arid conditions prevail. Although little is known of the ecological limitations of the subfamily, the species seem to have rather wide ranges and to occur under several and sometimes quite opposite environmental conditions. This is true not only of the different species but also in some cases of single species as, for instance, *A. melanocera,* collected on the high plateaus of central Mexico as well as in the limestone country of north Yucatan and in the tropical rain-forest of the Canal Zone.

As to their habitats, some species seem to be not uncommon, and *A. melanocera* or *A. candezei* are not rare in the collections; the majority of the species, however, are known only from the type specimens or typical series, and too little is known of their biology to allow general conclusions to be reached.

The fact that *A. melanocera* and *A. costaricensis* are reported feeding on the introduced *Cycas revoluta* seems to point out some degree of plasticity in the feeding habits.

I have collected one specimen of *A. candezei* in Isleta (Pueblo Indian Reservation in New Mexico, not far from Albuquerque). The area is a dry one, highly modified by irrigation and cultivation. The only specimen collected was found on the flowers of an unidentified Compositae and its behavior was similar to that of an adult *Orsodacna.* It was collected at about 11 A.M. on June 14, 1953. This specimen was not very active but tried to fly away and to bite with its mandibles in an attempt to escape. Several mutilated specimens of *Janbechynea elongata* in a vial, intercepted at Laredo, also show signs of using their mandibles when excited.

Aulacoscelis candezei does not stridulate nor jump and the

color of the living specimen is almost the same as that of the specimens in the collections.

I have studied some specimens of *Aulacoscelis högei* in Cornell University collections with the label "at light."

VARIABILITY

Although the samples studied are too small to show the infraspecific variability of the Aulacoscelinae, in the cases in which I have seen enough material, some color variability has been observed, culminating in *Aulacoscelis candezei*, in which there are both totally brick-red specimens and totally dark brown ones. Size seems to vary less than color, but one of the specimens of *A. tibialis* studied is nearly one third smaller than the other one. The pilosity and microsculpture of the dorsal surface appear quite constant within each species. If *A. costaricensis* and *A. melanocera* are two different species and not two races with different sexual dimorphism, *A. melanocera* is a very constant species in spite of being the most widely distributed one. All the studied specimens of it are almost alike. In the case of *A. candezei*, although it has not been possible to distinguish allopatric subspecies, a weak tendency has been observed towards predominance of dark specimens in the northern part of the range of the species from where no unicolorous red specimens have been seen. In *A. variabilis*, with similar type of chromatic variation, no such tendency has been detected.

CLASSIFICATION
(Figure 1)

Two divergent lines, represented by two different genera, may be recognized:

1. *Aulacoscelis*, restricted to the Central American area and adjacent parts of the southwestern United States and including the less specialized species.
2. *Janbechynea*, which includes more differentiated species and extends as far south as Peru, Brazil and Bolivia.

Aulacoscelis grandis may prove to represent an independent subgenus or even a genus; its inclusion in *Aulacoscelis* is doubtful and due to the fact that I have not seen a male of the species.

The remaining species of *Aulacoscelis* seem to be rather closely

related and the differentiation between them is not always easy.

The genus *Janbechynea* may be divided into two well defined subgenera, which represent two different levels of differentiation:

1. *Bothroscelis,* with the species *melyroides* and *fulvipes,* considered as connecting *Aulacoscelis* and *Janbechynea* but more closely related to the second, and
2. *Janbechynea s. str.* including the most atypical species of the subfamily and representing the most peculiar Aulacoscelinae. Although the three included species bear a close resemblance, they may be grouped as follows:
   2a. *J.* (*J.*) *elongata* from Mexico, in which the subgeneric characters are not fully expressed and in which sexual dimorphism consists in longitudinal costae on elytra in ♀.
   2b. *J.* (*J.*) *inverosimilis* and *J.* (*J.*) *paradoxa,* from Peru, Bolivia and Brazil, with a very peculiar type of ♀ (no ♂ ♂ are known of those species) and a tendency to modification of the metacoxae which, although already present in *J.* (*J.*) *elongata,* reaches its maximum in *J.* (*J.*) *paradoxa.*

The differentiation between the species of *Aulacoscelis* and those of *Janbechynea* seems to be closely correlated with the geographic distribution, and the isolation of the South American species has probably contributed to their greater distinctness.

The pronotal fold, peculiar to *Aulacoscelis,* is lost in *Janbechynea s. lat.* and the basal groove which remains in that genus as the only evidence of the fold tends to disappear; in *J.* (*J.*) *paradoxa* it is less conspicuous than in *J.* (*Bothroscelis*) *melyroides,* for instance.

NOTES ON PHYLOGENY

It is not probable that feeding on Cycadophyta is a derivative habit in Aulacoscelinae. The origin of the group probably precedes the appearance of the angiosperms. If so, the Aulacoscelinae are among the most ancient of living Chrysomelidae.

From the fact that the sagrid genus *Carpophagus* in Australia has also been reported on Cycadaceae and that it represents another and quite different line of evolution, it may be concluded

that the Chrysomelidae differentiated in early times (before the Jurassic period, for the gymnosperm-feeders) and that each one of the archaic living types is the relict of a different evolutionary line. Correlated with morphological and ethological characters, this may provide a clue to breaking up the immense number of chrysomelid species — of which more than 30,000 are already described — into smaller families of common but ancient ancestry. The uniformity of appearance of chrysomelids is undoubtedly due to their fairly uniform mode of life and requirements, but it must not be allowed to hide the fact of their very early divergence.

As for the center of origin of the Aulacoscelinae, the existing forms seem to have a relict distribution, and the data are insufficient for speculation. The isolation in South America of *Janbechynea inverosimilis* and *J. paradoxa*, which differ very much from the Central American *Aulacoscelis*, suggests a rather ancient and probably much wider distribution.

Key to the Genera

Prothorax with a short longitudinal fold on each side, extending from basal margin to beginning of disc. Scutellum triangular . . . . *Aulacoscelis*

Prothorax without such folds but with two basal grooves, contiguous to basal margin. Scutellum transverse and more or less triangular *Janbechynea*

I. Genus AULACOSCELIS Duponchel and Chevrolat

Duponchel and Chevrolat, 1843, p. 338; Stål, 1863, p. 341; Chapuis, 1874, p. 54; Jacoby, 1880, p. 1; Crowson, 1946, p. 83; Monrós, 1949, p. 547.

Etymology: From the Greek *aulacos* and *scelis* (fold and leg).

Type of genus: Aulacoscelis melanocera Dup. & Chevr., monobasic.

To define this genus, the general description of the subfamily may be supplemented as follows: Form more or less flattened, size from about 6.5 to about 12.5 mm. Integuments without metallic colors and rather soft. Head similar in both sexes. Prothorax with a short longitudinal basal fold on each side, extending from the basal margin to the posterior half of the disc and limiting a groove between this fold and the dilated basal margin of pronotum (fig. 15). Elytra irregularly punctured or

almost smooth, rarely with dense pubescence; sometimes with longitudinal costae which are always more visible in ♀. Scutellum triangular. Trochantin visible in antero-lateral angle of anterior coxae.

Key to the Species of Aulacoscelis

1. Elytra with dense and fine, rather long, pubescence throughout (fig. 13). Sides of pronotum subparallel, narrowed in front, and separated from disc by a broad and rather deep longitudinal depression. Pronotal surface uneven and with longitudinal tracts of decumbent pilosity. Black; elytra yellowish to reddish (fig. 37) . . . . . *grandis*

   Elytra glabrous or almost so (figs. 4-12). Pronotum of different shape and sculpture 2

2. Pronotum rather densely and deeply punctured and not shining (figs. 11 and 47) . . . . . *variabilis*

   Pronotum smooth and shining, almost impunctate 3

3. Elytra elongate and subparallel on basal 2/3; about as wide at base as in the middle 4

   Elytra more or less oblong elongate, broader towards middle than at base 6

4. Antennae slender; segments 8-10 distinctly longer than wide at apex (fig. 18) 5

   Antennae broader; segments 8-10 almost as wide at apex as long (fig. 17). Humeral elytral depression with long erect bristles. *högei*

5. Elytra with 3 more or less raised longitudinal carinae, of which the central one is shorter than the others and oblique; elytral disc brown or dark to a variable extent (fig. 16) . . . *candezei*

   Elytra without carinae or only with a sublateral, rather feeble one in the ♀; dorsal surface reddish unicolorous . . . *confusa*

6. Black; elytra yellowish (fig. 35) . . . . . *melanocephala*

   Coloration different 7

7. Sides of prothorax rather broadly expanded, its disc depressed. Yellow with apex of femora, tibiae and tarsi black (figs. 54-55) *tibialis*

   Sides of prothorax less expanded; its disc moderately convex. Reddish 8

8. Pronotum distinctly transverse, its sides very slightly curved. Form comparatively short and broad. Elytra not shining (fig. 36) . . . . . *sanguinea*

   Pronotum subquadrate, distinctly narrowed at base. Form more elongate and slender 9

9. Legs completely black. Elytra finely shagreened and with humeral longitudinal costa in ♀ ; shining and without costa in ♂ (figs. 21, 22) . . . . . *costaricensis*
Basal 2/3 of femora orange-red like rest of body. Elytra as in ♂ of *A. costaricensis* and without sexual dimorphism. . *melanocera*

1. Aulacoscelis candezei Chapuis

(Figures 4, 16)

Chapuis, 1874, p. 55, atlas, pl. 111, f. 6; Jacoby, 1880, p. 1; 1888, p. 2, pl. 35, f. 7; Crowson, 1946, p. 90.

A. purpurea Horn, 1892, p. 46; Crowson, 1946, p. 90 (new synonym).

United States. New Mexico (Horn): Las Vegas (1 ♂ Barber & Schwarz in USNM); Albuquerque (1 ♂ Wickham in USNM); Isleta (1 ♂ June 14, 1953 in col. Monrós, on flowers of Compositae). Arizona (3 col. Horn in PAS; 1 ♂ Ulke in CM): Walnut (1 ♂, 1 ♀ Wickham in USNM); Pinal Mts. (2 ♂ col. Van Dyke in CAS); Flagstaff (1, W). California: Needles (1 ♀ Wickham in USNM).

Mexico. Tepic (1 ♂ June 24, 1940 L. W. Saylor in CAS); Durango: Ventanas (3 ♂ Höge in col. Jacoby, col. Bowditch MCZ); Cerro de Plumas, San Miguel del Rio (Jacoby).

Guatemala (Chapuis).

Sexual dimorphism involves the basal segments of tarsi I and II and the last sternite.

Measurements. ♂ 6.8 x 2.1 to 8.7 x 2.8 mm.; ♀ 7.5 (Crowson) to 8.8 x 3.2 mm.

Form. Subcylindrical, moderately shining, sometimes with feeble violaceous metallic lustre. Color variable, from ochraceous yellowish with elytral disc more or less brownish, to obscure brown unicolorous with appendages black. Some intermediate specimens with head reddish brown, prothorax dark brown, elytral disc dirty brown with violaceous lustre on yellow ground; others with head dark brown, prothorax orange, elytra dirty brown, etc.

Punctuation. Head with some sparse, rather deep punctures, some with single short bristles. Prothoracic punctures smaller but more dense. Elytral punctures shallow, rather large and dense, most with one or two very short decumbent hairs.

Microsculpture. Minute granulation which somewhat diminishes the smoothness of the surface and is more visible in dark specimens or on dark areas.

Pilosity. Labrum with some long bristles on anterior margin. Sides of clypeus, antennae and sides of prothorax with whitish, decumbent, medium sized, moderately dense hairs; some sparse hairs of same type on postero-lateral pronotal margin. Elytra with some very short, decumbent setae, more abundant on basal third and placed one or two in most of the punctures. Ventral surface and legs with rather long but not dense pilosity, except on head and prosternum, which are glabrous and shining.

Head. With the buccal parts, somewhat elongate in shape. Antennae slightly longer than half the body; basal segment subglobose; apical one elongate rhombiform; intermediate ones obtusely triangular or subconical, slightly compressed, each one (except 2) distinctly longer than wide; segments 4-7 as much compressed as segments 8-10.

Pronotum. Feebly transverse. Sides slightly sinuate at basal third. Greatest width at anterior third. Disc slightly convex and without impressions.

Elytra. Elongate, subparallel in basal two-thirds, acute towards the apex, with apical margin subtruncate and somewhat dehiscent. Suture with a narrow raised border. Each elytron with a sublateral, longitudinal, distinct carina, which limits the lateral declivity, another one discal, parallel to the suture, and more or less fused to the preceding one at apex; and between them a third one, oblique, which begins at shoulder and ends near discal costa about mid-length of elytron. Carinae distinct in both sexes, but more so in the ♀.

Ventral surface and legs. Normal. Basal segments of tarsi I and II distinctly broadened in ♂. Last sternite subtruncate in ♂.

Male genitalia. Normal.

Host plant. One ♂ specimen of this species has been collected on flowers of Compositae in New Mexico (Monrós).

Remarks. Although the original description of this species is rather vague and although I have not been able to find out where the type specimens are, the figure given by Chapuis of *A. candezei* makes its identification rather sure. The identity of *A. candezei* and *A. purpurea* (of which I have seen holotype and 2 paratypes in PAS) is complete, and the latter name represents only a minor color variation without any significance.

It is the only known species of the genus with the described type of elytral coloration combined with the elytral costae.

2. Aulacoscelis högei Jacoby
(Figures 5, 17, 19, 20)

Jacoby, 1888, p. 3; Crowson, 1946, p. 90 (pars).

Mexico. Guerrero: Chilpancingo (1 ♀ cotype #8448 Höge in col. Jacoby, col. Bowditch MCZ; 5 ♀ col. Bowditch MCZ); Mexcala (1 ♂ allotype, 2 ♀ June 29, 1951, H. E. Evans in CU; 1 ♂, 2 ♀ col. Monrós *ex* CU, collected at light).

Sexual dimorphism as in *A. candezei.*

Measurements. ♂ 8.1 x 2.9 mm.; ♀ 9.2 x 3.2 mm.

Form. Similar to *A. candezei.* Color yellowish orange to brick red, with antennae, palpi, apices of femora, tibiae, and tarsi black.

Punctuation. Punctures on head and prothorax as in *A. candezei;* on elytra smaller and feebler.

Microsculpture. Of same type as *A. candezei,* but less conspicuous.

Pilosity. Head and pronotum like *A. candezei.* Elytra with some sparse, erect, short, golden bristles.

Head. Of same type as *A. candezei.* Antennae slightly shorter than half the body, of same general type as *A. candezei,* but segments shorter and more triangularly compressed, especially 8-10 which are almost as wide at apex as long. The whole antenna is distinctly more robust than in *A. candezei.*

Pronotum. About as wide as long, with greatest width at middle; otherwise similar to that of *A. candezei.*

Elytra. Elongate, subparallel in basal two thirds, acute towards the apex, with apical margin almost entire. Suture with a narrow raised border. Carinae as in *A. candezei,* but less distinct and almost invisible in ♂ and sometimes only the lateral one is visible in ♀.

Ventral surface and legs. Normal. Basal segments of tarsi I and II broadened in ♂, but less so than in *A. candezei.* Last sternite subtruncate in ♂.

Male genitalia. Normal (figs. 19, 20).

Remarks. This species is very similar to the following one (*confusa, q.v.*). From *A. candezei,* to which it is also closely related, *A. högei* may be distinguished by the somewhat shorter and distinctly broader antennae with more compressed segments, as well as by the less raised elytral costae and the short, erect elytral bristles, absent in *A. candezei.*

3. Aulacoscelis confusa n.sp.
(Figures 6, 18)

A. högei Jacoby, 1888, p. 3, pl. 35, f. 6; Crowson, 1946, p. 90 (pars.).

"Canada: Van Couver Island" (1 allotype ♂ col. Jacoby, col. Bowditch MCZ, in bad shape; 1 paratype ♀ same data, with label "type 8448 of *A. högei.*")

Mexico. Tehuantepec (1 holotype ♀ #29238 in col. Bowditch MCZ; 1 paratype ♀ same data; 1 paratype ♀ T. F. Sumichrast in col. Monrós, *ex* Bowditch MCZ).

This species is so closely related to *A. högei,* with which it has been confused, that only the differences need to be pointed out.

Measurements. ♂ (allotype) 7.8 x 2.8 mm.; paratype ♀ 8.8 x 3.5 mm.

Color. Like *A. högei,* but dark parts dark brown (not black).

Pilosity. Elytra with some sparse, erect, rather long bristles in humeral depression, more conspicuous when observed from the side.

Head. Antennae as in *A. candezei, i.e.* more slender, somewhat longer, and less compressed than in *A. högei* (fig. 18).

Elytra. Completely without costae in ♂ and with only 1 feeble one in ♀, corresponding to the discal-lateral one in *A. högei* and *A. candezei.*

Legs. Basal segments of tarsi I and II somewhat broadened in ♂, but less so than in *A. högei* and much less than in *A. candezei.*

Male genitalia. Not examined.

Remarks. This species has been confused with the preceding one by Jacoby and probably also by Crowson, so that it is not possible to accept the localities they give without checking each one of them.

In spite of being very closely related, *A. confusa* may be distinguished from *A. högei* by its longer and more slender antennae, and also by the presence of erect bristles on the humeral depression of the elytra, these bristles being entirely absent in *A. högei.* The whitish bloom described by Jacoby on *A. högei* actually occurs on the present species and not on the real *A. högei.* From *A. candezei,* to which it is also more or less similar, the present species may be distinguished by color as well as by near absence of elytral costae and presence of erect bristles on the humeral

depression. From *A. melanocera* and related forms of similar coloration, it differs in being more elongate and slender.

The specimens recorded by Jacoby as *A. högei* from Vancouver Island belong to the present species as does the one illustrated in the *Biologia Centrali Americana* under the name *A. högei*. I have examined the specimens labeled "Van Couver Island" and they completely agree with the typical specimens from Tehuantepec. It is almost certain that the "Vancouver Island" specimens are wrongly labeled.

4. Aulacoscelis melanocera Duponchel and Chevrolat (Figures 7, 15, 31 to 34)

Duponchel and Chevrolat, 1843, p. 338; Stål, 1863, p. 342; Jacoby, 1880, p. 2; Crowson, 1946, p. 90; Monrós, 1949, figs. 6, 9, 14, 21, 23.

Mexico (Duponchel and Chevrolat, Stål); Oaxaca, N. Yucatan (Jacoby); S. Mexico (Crowson); Oaxaca: Almoloya (1 ♂, 2 ♀ F. Knab in USNM, det. *A. högei*); Vera Cruz (1 USNM, W. Anderson det.); Nogales (1 ♀ June 16, 1905 F. Knab in USNM); Tampico (1 ♂, 1 ♀ June 1910 Palmer in USNM); N. Yucatan (1 ♀ USNM, Jacoby det.); Mexico (1 Bowditch leg. USNM; 3 col. Bowditch MCZ; 3 col. Jacoby in col. Bowditch MCZ); Paristlahuaca (1 Sallé leg. in col. Jacoby, col. Bowditch MCZ); Tamazunchale (5 col. USNM, intercepted at Laredo); Cerro de Plumas (3 Höge leg. in col. Jacoby, col. Bowditch MCZ); Huauchinango (1 col. Bowditch MCZ); Oaxaca (2 Höge in Bowditch MCZ); N. Yucatan (1 Gaumer leg. in col. Jacoby, col. Bowditch MCZ); Jalapa (Flohr leg. in col. Jacoby, col. Bowditch MCZ); Vera Cruz: Atoyac (1 col. Jacoby, col. Bowditch MCZ).

Guatemala. Chacoj, Panzos (Jacoby); Vera Paz: Chacoj (4 Champion in col. Jacoby, col. Bowditch MCZ).

Honduras. Siguatepeque (3 Rittenhouse in USNM).

Nicaragua. Managua: La Calera (3 ♂, 4 ♀ May 14, 1952 R. B. Swain in USNM).

Panama (Crowson). Volcan de Chiriqui (Jacoby); Panama city (3 col. Bowditch MCZ).

Canal Zone. Summit (1 ♂, 2 ♀ June 12, 1928 Zeteck in USNM).

El Salvador (85 S. Calderon in USNM).

Published localities in Costa Rica are not listed as it seems probable that they really concern *A. costaricensis*.

Sexual dimorphism as in *A. candezei*.

Measurements. ♂ 7.7 x 2.8 mm.; ♀ 8.2 x 3.1 mm. (somewhat variable, plus and minus)

Form. Oblong, rather short, moderately convex and shining, broader and more depressed than preceding species. Red, with antennae (except basal segments), tarsi, tibiae and apices of femora black. The red color varies from pale orange to blood red. In one of the specimens examined the legs are completely black.

Punctuation. Head and prothorax almost impunctate. Elytral punctures small and moderately dense, smaller towards apex.

Microsculpture. Surface smooth and shining, micro-reticulation not visible.

Pilosity. Head and prothorax as in preceding species. Elytra with some very sparse, erect, short bristles, especially on basal half. Ventral pilosity whitish.

Head. As in preceding species. Antennae little longer than half the body, of the general type of *A. candezei* but somewhat less slender (and in that respect more similar to *A. högei*).

Pronotum. Very slightly transverse, of same shape as in preceding species.

Elytra. Elongate, suboblong, separately rounded at apex and without apical sutural denticle. Suture with a narrow raised border. Sides moderately expanded. Surface moderately shining, moderately convex, with a distinct post-scutellar depression and a humeral sulcus. In the ♀, the elytra show a feeble and sometimes almost obsolete humeral carina which is totally absent in the ♂.

Ventral surface and legs. Normal. Basal segments of tarsi I and II broadened in ♂. Last sternite notched in ♂.

Male genitalia. Normal (figs. 33, 34).

Host plants. Cycas revoluta (specimens from El Salvador in USNM); cycad plant (specimens from Tamazunchal in USNM); palm (specimen from Honduras in USNM).

Remarks. This is the type species of the genus and also one of the most typical *Aulacoscelis.* It is the most common species in collections and the most widely distributed one. The resemblance between the present species and *A. högei* or *A. confusa* is only superficial; the body shape as well as the elytral punctures are quite different.

5. Aulacoscelis costaricensis Bechyně
(Figures 8, 21 to 30)

Bechyně, 1950, p. 237.

Costa Rica. San Carlos (9 ♂, 2 ♀ Schild & Burgdorf in USNM, topotypes; 1 ♂ with label "A. melanocera"); Naranjo (1 ♀ Bowditch leg. USNM); Aleluya (2 ♂, 4 ♀ E. Morales M. in USNM); Concavas (7 ♂, 9 ♀ May 17, 1938, Lankester leg. col. Nevermann in USNM); San José (2 ♂ Underwood in col. Bowditch MCZ).

Sexual dimorphism involves the basal segments of tarsi I and II, the elytra, and the last sternite

Measurements. ♂ 8.2 x 2.9 mm.; ♀ 8.4 x 2.8 mm.

Form. As in *A. melanocera.* Color identical, except legs entirely black, and red color always somewhat darker.

Punctuation and pilosity. As in *A. melanocera.*

Microsculpture. Male smooth and shining, without visible microsculpture; ♀ with a fine shagreen on elytra which makes them less shining.

Head and pronotum. As in *A. melanocera.*

Elytra. Male as in *A. melanocera.* Female somewhat broader, subtruncate at apex, and with a distinct longitudinal sublateral carina beginning at shoulder and ending at anterior third.

Ventral surface and legs. As in *A. melanocera.*

Male genitalia. Normal (figs. 27 to 29).

Host plant. Nevermann's specimens in USNM with label "Frisst an Blatt von *Cycas revoluta.*"

Remarks. The main difference between the present species and *A. melanocera* is the different type of sexual dimorphism; the difference in coloration of the legs seems not important since specimens of *A. melanocera* occur with legs completely black. Whether these two forms are specifically different or whether they are merely subspecies of one species, must be decided by study of more and more significant material.

6. Aulacoscelis sanguinea Jacoby
(Figures 9, 36, 39)

Jacoby, 1888, p. 5, pl. 35, f. 10; Crowson, 1946, p. 89.

Mexico. Guerrero: Chilpancingo (1 ♂ col. Jacoby in Bowditch MCZ, cotype).

Sexual dimorphism (according to Crowson) involves the elytral apex.

Measurements. ♂ 8 x 2.8 mm

Form. As in *A. melanocera.* Antennae entirely black.

Punctuation and pilosity. As in preceding species.

Microsculpture. Elytra with distinct microgranulation, less shining than in *A. melanocera.*

Head. Antennae somewhat longer and more slender than in *A. melanocera.*

Pronotum. Slightly transverse; sides very slightly arcuate; greater width at middle; anterior and basal margins of almost equal width; sides not constricted at base.

Elytra. Rather broad and short, widest behind middle, with lateral margins expanded. Humeral impression almost obsolete. According to Crowson, the ♀ has an apical denticle on elytral suture, which distinguishes it from the ♂.

Ventral surface and legs. Normal.

Male genitalia. Normal (fig. 39).

Remarks. I have examined only one ♂ to which the preceding description refers.

This species, although appearing similar to *A. melanocera* and *A. costaricensis,* may be easily distinguished by the different shape of pronotum and less shining elytra, which are also shorter and broader.

7. Aulacoscelis melanocephala Jacoby
(Figures 10, 35, 38)

Jacoby, 1877, p. 510; 1880, p. 2, pl. 1. f. 1.

Guatemala. (1 ♂ holotype in col. Jacoby, col. Bowditch MCZ).

Measurements. ♂ 9.0 x 3.3 mm.

Form. As in *A. sanguinea.* Color black, with a feeble reddish tint dorsally and the elytra ochraceous yellow.

All the characters almost identical with *A. sanguinea,* from which it is distinguished by different ♂ genitalia (fig. 38).

8. Aulacoscelis variabilis Jacoby
(Figures 11, 40 to 53)

Jacoby, 1888, p. 4, pl. 35, f. 8, 9; Crowson, 1946, p. 90.

Mexico. Hidalgo: Pachuca (4 ♂, 7 ♀ Höge leg. in col. Jacoby col. Bowditch

MCZ, cotypes; 3 Höge leg. USNM, Jacoby det., cotypes); Sierra de Durango (3, col. Bowditch MCZ); Real del Monte (1, Flohr leg. col. Jacoby, col. Bowditch MCZ, cotype).

Sexual dimorphism involves only the last sternite. Basal segments of tarsi almost equal in both sexes. No sexual dichromism.

Measurements. 8.4 x 2.9 mm. to 8.7 x 3 mm.

Form. Oblong-elongate, rather depressed, not shining. Color variable: dirty brown either unicolorous (about half the specimens examined) or with prothorax and elytral epipleurae orange-red to a variable extent.

Punctuation. Cephalic punctures rather dense and deep, especially towards base, most of them with a short, white, oblique bristle. Pronotal punctures sparser, especially on disc, but denser and deeper than in preceding species. Elytral punctures closer than those of prothorax, most with a very short, white bristle directed obliquely backwards.

Microsculpture. Dorsal surface of body with a minute reticulation which makes it dull.

Pilosity. Of the same type as in preceding species; elytra with some longer hairs on shoulders, and entirely covered with the very short ones already described.

Head. Antennae about half the length of body, slightly compressed, of the type of *A. candezei;* antennal pilosity shown in Figures 49 to 51.

Pronotum. About as wide as long. Sides slightly sinuate at basal third. Disc rather depressed and sometimes with two shallow, irregularly rounded depressions.

Metendosternite. Shown in Figure 53, similar to that of *A. candezei* figured by Crowson.

Elytra. Elongate, subparallel in basal two thirds and acute at apex, where very slightly dehiscent; without sutural denticle. Suture narrowly bordered; sides moderately expanded, more so in basal half. Surface rather flat, each elytron with a slight postscutellar depression and another, elongate one, on the shoulder.

Ventral surface and legs. Normal, similar in both sexes. Last sternite of ♂ deeply notched.

Male genitalia. As shown in Figures 44 to 46.

Remarks. This is a very easy species to recognize because of the dull pronotum, the rather depressed body, and the dense dorsal punctures.

9. Aulacoscelis tibialis Jacoby

(Figures 12, 54 and 55)

Jacoby, 1888, p. 3, pl. 35, f. 2; Crowson, 1946, p. 88.

Guatemala. Vera Paz: San Juan (Jacoby); Senahú (1 ♀ cotype Champion leg. in col. Jacoby, col. Bowditch MCZ).

British Honduras: M-tee Dist. (1 ♂, 1 ♀ August 10, 1906 col. Bowditch MCZ).

Sexual dimorphism involves the tarsi, abdomen and elytra.

Measurements. ♂ from Honduras 10.6 x 3.7 mm.; ♀ cotype 12.6 x 5 mm; ♀ from Honduras 7.4 x 3 mm.

Form. Oblong-elongate, rather flat, moderately shining. Pale yellow to orange-yellow; antennae (except basal segments), palpi, tarsi, tibiae, and tips of femora black

Punctuation. Cephalic punctures sparse and superficial, very few of them with short, decumbent bristles. Prothorax almost impunctate. Elytral punctures sparse and superficial, with some sparse decumbent hairs in them at base and sides.

Microsculpture. Dorsal surface minutely shagreened, but this does not affect the lustre and is visible only under strong magnification.

Pilosity. Dorsal surface practically glabrous.

Head. As shown in Figure 55. Antennae half the body length, with segments 3-7 somewhat compressed, increasing in length from second to apical one.

Pronotum. Rather depressed, shape as shown in Figures 54 and 55.

Elytra. With sexual dimorphism. Male, oblong-oval, elongate, with maximal width behind middle, the surface practically without irregularities, except for the humeral callus and the sublateral depression; ♀ with 3 longitudinal costae of which the external one is long and well developed, the internal one short and very feeble, and the intermediate one visible especially on the shoulder; between the last carina and the lateral declivity there is a rather inconspicuous fold.

Ventral surface and legs. Normal. Basal segments of tarsi I and II broadened in ♂. Last sternite as in preceding species.

10. Aulacoscelis grandis Jacoby

(Figures 13, 37)

Jacoby, 1888, p. 6, pl. 35, f. 1 ♂; Crowson, 1946, p. 88.

Mexico. Durango: Ventanas (Jacoby); Mexico (1 ♀ Flohr leg. col. Jacoby col. Bowditch MCZ).

Measurements (♀). 10.9 x 3.2 mm.

Form (♀). Elongate oval, depressed; widest behind middle. Black, elytra orange-brownish.

Punctuation. Head with some small punctures, each with a long hair. Prothorax with punctures only at base of hairs. Elytral punctures moderately dense and deep.

Microsculpture. Head, prothorax, and scutellum smooth and shining; elytra inconspicuously finely shagreened.

Pilosity. Labrum with long, white setae directed forward. Interocular depression with long, crossed hairs; postocular region with similar hairs, directed forward. Prothorax with two longitudinal irregular rows of hairs on each side of disc, and a dense pilosity on all margins. Scutellum with some sparse hairs. Elytra with a fringe of bristles along the margin, longer towards apex; and surface with rather dense, rigid bristles, directed backwards. Pilosity of ventral surface, antennae, and legs fine and moderately dense.

Head. Elongate, depressed; eyes small and rather prominent; postocular region slightly constricted and with a transverse impression on each side; interocular and interantennal space depressed, limited on each side by a thick carina; clypeus on a lower level than rest of head. Antennae half body length, with segments 3-8 moderately, triangularly expanded (the fourth is the most expanded, and from it the antenna diminishes in width toward apex and base).

Pronotum. About as long as wide, with sides somewhat convergent anteriorly. Anterior margin feebly bilobed. Sides with narrow, elevated margins, separated from disc by broad and shallow depressions. Base subtruncate, narrowly bordered. Disc scarcely convex, with feeble impressions arranged as shown in Figure 37, and with a short but distinct longitudinal carina on each side at base.

Elytra. Elongate, depressed, gradually broadened in basal two thirds, then conjointly and broadly rounded. Suture nar-

rowly bordered. Lateral margins horizontally expanded and separated from the disc by very distinct longitudinal impressions, which disappear towards apex.

Ventral surface and legs. Normal.

Remarks. The specific name of this species may lead to confusion, as *A. tibialis* is larger than the present one. *A. grandis* is very peculiar looking, and its prothorax as well as the antennal shape easily distinguish it from the other *Aulacoscelis.*

II. Genus Janbechynea Monrós

Monrós, 1953, p. 21.

Etymology: Named for Jan Bechyně, a specialist on Chrysomelidae.

Type of genus: Janbechynea paradoxa Monrós, monobasic and orthotype.

The addition of some other species to the present genus makes the following modification of the generic description necessary: Form elongate and somewhat acute. Head distinctly broader in ♂. Antennae at least as long as half length of body in both sexes; segments elongate-triangular, not much expanded internally. Pronotum with a basal elevated margin, and in front of it, on each side, a deep circular impression (fig. 14); pronotal disc without longitudinal fold at base. Scutellum transverse-rectangular. Elytra densely covered with fine pilosity. Legs rather long and slender. Male genitalia with median lobe prolonged into a long median projection.

This genus, thus redescribed, may be distinguished from *Aulacoscelis* by the lack of pronotal folds, the different shape of the scutellum, the different type of ♂ genitalia, and the sexual dimorphism of the head. In *Aulacoscelis* (except *A. grandis,* which is doubtfully included in that genus) the elytra are glabrous or almost so. In all the species of *Janbechynea* they are covered by dense pilosity.

The present genus is divided into two subgenera, distinguished in the following key.

Elytral apices rounded in both sexes, moderately dehiscent. Elytra not sexually dimorphic. Size smaller (up to 10 mm.). Abdomen of normal length in both sexes . . . *Bothroscelis*

Elytral apices in the ♀ prolonged into divergent points and

strongly dehiscent. Elytra with sexual dimorphism. Size larger (over 13 mm.). Abdomen shortened, especially in the ♀. . . *Janbechynea s. str.*

A. subgenus BOTHROSCELIS nov.

Etymology: From the Greek *bothros* (groove) and *scelis* (leg).

Type of subgenus: Aulacoscelis fulvipes Jacoby.

The differences between the present subgenus and *Janbechynea s. str.* are given in the preceding key.

Bothroscelis contains species which are less differentiated from *Aulacoscelis,* while *Janbechynea s. str.* includes the most specialized species and those which differ most from the rest of the Cyclica.

The subgenus *Bothroscelis* includes two known species.

Elytral pubescence decumbent and dense. Prothorax densely and deeply punctured, with distinct pubescence along the borders (figs. 64, 65) . . . . . *fulvipes*

Elytral pubescence recumbent and sparser. Prothorax with only some punctures on marginal areas and some scattered bristles on lateral borders (fig. 57) . . . . . *melyroides*

1. JANBECHYNEA (BOTHROSCELIS) MELYROIDES (Crowson) (Figures 57, 63)

Aulacoscelis melyroides Crowson, 1946, p. 89.

Mexico. Guerrero: Chilpancingo, 4600 ft. H. H. Smith (Type locality; 1 ♂, 1 ♀ paratypes in coll. Monrós, *ex* British Museum).

Sexual dimorphism involves the head and elytral pilosity.

Measurements. ♂ 6-7 mm; ♀ 5-7 mm. (according to Crowson).

Form. Elongate-oblong, subdepressed, elytra subparallel. Shining, rather densely pubescent on elytra. Color variable (sexual dichromism?): ♂ dark brown, almost black on head and elytra, paler and reddish on legs and antennae, mouth parts yellowish, pronotum yellow with a discal, ill-defined, large brown patch and elytral epipleurae pale yellow; ♀ with elytra and basal half of head deep black, rather shining, pronotum unicolorous yellow, anterior half of head yellow; otherwise, including elytral epipleurae, as in ♂.

Punctuation. Cephalic punctures sparse, rather deep, most

with fine, oblique bristles. Pronotal punctures of same type, very distinct but not dense on disc. Elytral punctures shallower but closer than those of head and prothorax, with hairs.

Microsculpture. Head and pronotum smooth and shining; elytra with a fine but distinct microgranulation.

Pilosity. Head with some long setae on clypeus and labrum and shorter ones rather sparse on front and interocular area. Antennal pilosity of same type as in *Aulacoscelis.* Prothorax almost glabrous except for fringes of bristles on anterior and basal margins and some sparse bristles near basal angles at sides. Scutellum with some long, decumbent setae. Elytra dimorphic: male with rather long, moderately dense hairs, directed obliquely backwards and almost uniformly distributed, lateral margins with fringes of short, dense bristles; ♀ with pilosity longer, finer, and more erect, especially on basal half; lateral fringes longer and finer.

Head. Male almost as broad as long and of the normal Aulacosceline-type. Antennae somewhat longer than half the body, its segments elongate and rather slender, 5-11 more than twice as long as broad at apex. Female narrower and more elongate than ♂. Antennae shorter than half body length and somewhat more robust than in ♂ but of same general form.

Pronotum. In ♀ of normal Aulacosceline-type, as (for instance) in *A. melanocera;* in ♂ more subparallel, with less conspicuous lateral-basal constriction. Basal fold and discal impressions absent; basal grooves distinct and deep.

Elytra. Elongate, subparallel in basal two thirds, moderately acute towards apex, where they are somewhat dehiscent. Sutural angles without denticles. Suture with a narrow raised border. Sides slightly horizontally expanded. Surface rather flat in both sexes, with an inconspicuous, longitudinal, short humeral carina in the ♀ but completely absent in the ♂.

Ventral surface and legs. Normal. Abdomen somewhat shortened in ♀.

Remarks. The erect elytral pilosity, together with the smooth pronotum and the small size, easily distinguish the present species from *J. fulvipes,* with which it has been confused.

2. Janbechynea (Bothroscelis) fulvipes (Jacoby)

(Figures 56, 64 to 71)

Aulacoscelis fulvipes Jacoby, 1888, p. 4; Crowson, 1946, p. 90.

Aulacoscelis femorata Jacoby, 1888, p. 5, pl. 35, f. 3 ♂, 4 ♀; Schaeffer, 1905, p. 168; Crowson, 1946, p. 88 (new synonym).

Aulacoscelis ventralis Schaeffer, 1933, p. 297.

United States. Arizona: Huachuca Mts. (4 ♂, 3 ♀ July, 1905 C. W. Leng in Hopping col. CAS; 3 ♀ col. Schaeffer in USNM): Carr Canyon (1 ♂ J. O. Martin in CAS; 1 ♀ August 6, 1924 E. P. Van Duzee in CAS); Cochise Co.: Palmerlee (1 ♂, 1 ♀ col. Schaeffer in USNM).

Mexico. Chilpancingo (Jacoby), Capulalpam (Jacoby); Durango: Ventanas (1 ♂, 7 ♀ cotypes col. Jacoby in col. Bowditch MCZ); Chihuahua (8 ♂, 5 ♀ Wickham leg. in col. Bowditch MCZ); Guanajuato (1 Sallé leg. col. Jacoby in col. Bowditch MCZ).

Sexual dimorphism involves the last sternite, head, antennae, and somewhat shortened abdomen in ♀. Basal segments of tarsi almost equal in both sexes.

Measurements. 8 x 2.8 mm. to 8.7 x 3 mm.

Form. Subcylindrical, acute towards apex. Color variable, from testaceous with apices of femora and bases of tibiae brown, to reddish-brown with legs and apex of abdomen yellowish brown, with a wide variety of intermediate colorations (head dark brown, prothorax orange, elytra reddish brown; head and prothorax orange, elytra grayish brown, etc.)

Punctures. Head densely and rather deeply punctured, especially near base; most of the punctures with short decumbent bristles. Elytral punctures rather close, each with a long, decumbent hair. Prothoracic punctures variable, from rather sparse and shallow to dense and deep, especially on anterior angles.

Microsculpture. Microgranulation present without dulling the surface, but hidden by the pilosity on prothorax and elytra.

Pilosity. Head with some decumbent, sparse, short hairs. Scutellum and elytra covered with moderately long, rather dense, decumbent, slightly depressed hairs. Pronotal pilosity variable; specimens with dense punctuation have also dense pilosity, especially on sides; in others the pilosity is sparser but basically similar.

Head. Transverse, interantennal depression U-shaped, open behind, rather deep. Clypeus at level of antennal border. Anten-

nae of same type as in *Aulacoscelis variabilis,* longer than half the body, moderately expanded.

Prothorax. Somewhat transverse, with anterior margin slightly broader than basal one. Sides slightly constricted in basal third in both sexes, but more so in ♀. Disc with two transverse depressions near anterior angles, more impressed on specimens with abundant pilosity.

Elytra. Elongate, acuminate in apical third, with the border obliquely truncate at apex on suture, without sutural denticle. Suture narrowly bordered. Sides not expanded, narrowly bordered. Dorsal surface moderately convex, with a shallow, longitudinal humeral depression, without carinae in both sexes.

Ventral surface and legs. Normal.

Male genitalia. As shown in Figures 70 and 71; median lobe prolonged into an acute point.

Remarks. Specimens in the Schaeffer collection in USNM are the types (holotype ♂, allotype ♀ and 3 paratypes) of *Aulacoscelis ventralis.* One specimen in MCZ with label "Type 8449" of *Aulacoscelis femorata.* One specimen in MCZ with label "Type 8447" of *Aulacoscelis fulvipes.*

The identity of *A. femorata* with *A. fulvipes* has been established by comparing the types of both and by study of a series of intergrading specimens. *A. femorata* is based on a pale colored ♂ with sparse pronotal punctures and pilosity; *A. fulvipes* on a brown ♀ with dense pronotal punctures and pilosity, but no real structural differences have been discovered between the specimens with these two types of sculpture, and they intergrade in series from the same localities. As for *A. ventralis,* its identity with *A. femorata* has been pointed out by Crowson, and the study of the types confirms it.

B. subgenus JANBECHYNEA s. str.

Key for the separation of the species (based on ♀♀)

1. Elytra with three longitudinal discal costae. Orange; elytra brownish. Metacoxae normally shaped . . . . . *elongata*
   Elytra with two transverse discal tubercles. Brick-reddish, elytra more or less metallic bluish 2
2. Metacoxa prolonged into a triangular plate which reaches end of

third abdominal sternite . . . . . *paradoxa*
Metacoxa shorter, prolonged into an oblong, stout projection not longer than first abdominal sternite . . . . *inverosimilis*

3. Janbechynea (s. str.) elongata (Jacoby)

(Figures 58, 72, 75 to 78)

Aulacoscelis elongata, Jacoby, 1888, p. 5, pl. 35, f. 5; Crowson, 1946, p. 88.
Mexico. Playa Vicente (Jacoby); San Luis de Potosí: Tamazunchale (2♂, 1♀ allotype May 20, 1952 intercepted at Laredo, Texas, feeding on Cycads, in USNM collection).

Sexual dimorphism strong

Measurements. ♂ 16 x 4.3 mm.; ♀ (allotype) 16.2 x 4.4 mm.

Form. Distinct in both sexes. Color pale orange; elytra pale brown, yellowish at suture and lateral margin; antennae (except basal segments), tibiae, tarsi and apices of femora black; elytral pilosity pale.

Punctuation. Cephalic punctuation moderately dense and deep; pronotum almost without punctures; scutellum and elytra with punctures hidden under pilosity.

Microsculpture. Elytra minutely shagreened in both sexes.

Pilosity. Head and pronotum glabrous and shining, except for some bristles on basal margin of pronotum. Scutellum and elytra with long, dense, decumbent pilosity, sparser on disc in ♀.

Male. Head as described for subfamily, nearly as broad as pronotum. Antennae two thirds as long as the body, with intermediate segments rather elongate. Pronotum as long as wide, with maximum width at middle. Sides distinctly sinuate in basal half. Basal margin with a rather deep, small groove on each side. Elytra narrowed in apical third, somewhat dehiscent at apex, which is rounded, practically without irregularities, except for the somewhat expanded sutural and lateral margins. Abdomen less than one quarter shorter than elytra, its last segment with a rather deep but narrow, angular incision. Mesotibiae somewhat curved. Basal segments of tarsi I and II broadened. Median lobe of genitalia very long and slender, prolonged into a median elongate hook curved dorsally, in which no median suture is visible.

Female (allotype). Head distinctly narrower than pronotum. Antennae about one half length of body. Pronotum widest before

middle. Basal grooves not as deep as in ♂. Elytra longer than in ♂, very acute towards apex, and with a long, dehiscent, acute external angle. Disc with three distinct, longitudinal, subparallel costae, the outer one limiting the lateral declivity, the inner one shortest. Abdomen shortened; about one third shorter than elytra; its last segment with a short, obtuse, apical, angular projection. Mesotibiae almost straight. Tarsi not broadened.

Remarks. Although Jacoby mentions the existence of a longitudinal pronotal groove, none of the specimens studied has it.

4. Janbechynea (s. str.) inverosimilis n. sp.
(Figures 59, 61, 62, 73, 79)

Peru. Chanchamayo (1 holotype ♀ #29237 in col. Bowditch MCZ).

Measurements. ♀ holotype 16 x 5.8 mm.

Form. Elongate and acuminate at apex. Color brick-red; elytra blue-greenish, with moderate metallic shine. Antennae (except basal segments), hind legs, tibiae, tarsi, and apices of femora of other legs black. Scutellum paler than pronotum. Elytral pilosity black.

Punctuation. As in *J. elongata.*

Microsculpture. Elytra minutely shagreened.

Pilosity. As in *J. elongata* but elytral hairs finer and shorter.

Head. Similar to that of *J. elongata* ♀ but more elongate and with mandibles more projecting.

Pronotum. About as long as wide, widest slightly before middle. Sides moderately rounded, not sinuate at base. Basal grooves not so deep as in *J. elongata.*

Scutellum. Very distinctly transverse, broader and more rectangular than in *J. elongata.*

Elytra. Of same general form as in ♀ of preceding species, but more elongate. Disc with 2 transverse tubercles, the anterior one larger and higher.

Legs. As in ♀ of *J. elongata.* Metacoxae swollen, their posterior margins extended in irregular curves.

Abdomen. Very short; first segment with a longitudinal, excavated, pubescent tract.

Remarks. A very large, strange-looking species, easy to recognize.

5. Janbechynea (s. str.) paradoxa Monrós
(Figures 60, 74)

Monrós, 1953, p. 21, figs. 1-8.

Bolivia. Santa Cruz (1♀ holotype, 2♀ paratypes in Museum Frey, München; 2♀ paratypes in col. Monrós, *ex* Frey).

Brazil. Chapada (1♀ CM; 1♀ col. Monrós *ex* CM).

This species so closely resembles *J. inverosimilis,* that only the differences need to be pointed out.

Size somewhat smaller (13 to 14 mm. x 5 mm.); coloration same but somewhat paler and elytra duller and more violaceous, with extreme base orange reddish in the specimens from Chapada. All femora with basal halves orange-reddish. Pronotal grooves shallower than in *J. inverosimilis.* Elytral pilosity finer; elytral tubercles less raised. Metacoxae extended as triangular plates of which the lateral margins reach the posterior edge of the third ventral segment. Those plates are flat and finely pubescent ventrally.

Remarks. This species could be confused with the preceding one, but is easily distinguished by the very peculiar shape of the metacoxal plates.

SUMMARY

1. The history, characters, systematic position and geographic distribution of the Subfamily Aulacoscelinae are described and the relationships with the other Chrysomelidae are discussed.
2. Host plants for some species, and some observations on the habits of *Aulacoscelis candezei* Chap., are reported for the first time.
3. Some remarks on the probable phylogeny, variability and significance of the group are added.
5. Keys for the genera, subgenera and species are given, and all the species redescribed.
6. *Aulacoscelis melanocera* is credited to Duponchel and Chevrolat, 1842, and not to Stål, 1865 as is usually done.
7. The male genitalia of several species are described and illustrated for the first time, and so is the pilosity and sculpture of the dorsal surface. The habitus of most of the species is figured from typical material.

8. The genus *Janbechynca* Monrós is redescribed and its limits broadened.
9. *Bothroscelis* (type *Aulacoscelis femorata* Jac.) is described as a new subgenus of *Janbechynea.*
10. New distributions: *Aulacoscelis melanocera* Dup. & Chevr. for British Honduras and Nicaragua; *A. tibialis* Jac. for British Honduras; *Janbechynea paradoxa* Monrós, for Brazil.
11. New combinations: *Aulacoscelis melyroides* Crowson and *A. fulvipes* Jac. are transferred to *Janbechynea* (*Bothroscelis*); and *Aulacoscelis elongata* Jac., to *Janbechynca s. str.*
12. New species: *Aulacoscelis confusa* and *Janbechynea* (*s. str.*) *inverosimilis.*
13. New synonyms: *Aulacoscelis candezei* Chap. (=*A. purpurea* Horn); *Janbechynea* (*Bothroscelis*) *fulvipes* (Jac.) (=*Aulacoscelis femorata* Jac.).

    The identity of *Janbechynea fulvipes* (Jac.) and *Aulacoscelis ventralis* Schaeffer is confirmed by type examination.
14. Allotypes described: ♂ of *Aulacoscelis tibialis* Jac., ♀ of *Janbechynea elongata* (Jac.).
15. A bibliographical list intended to cover the whole subfamily is appended.

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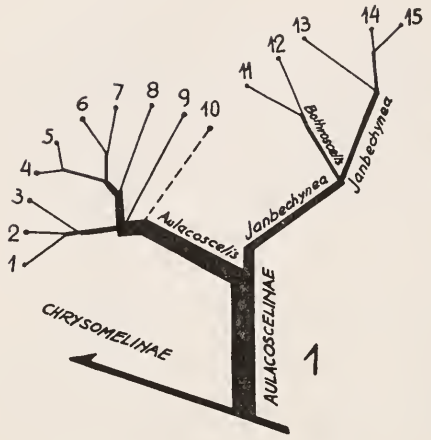


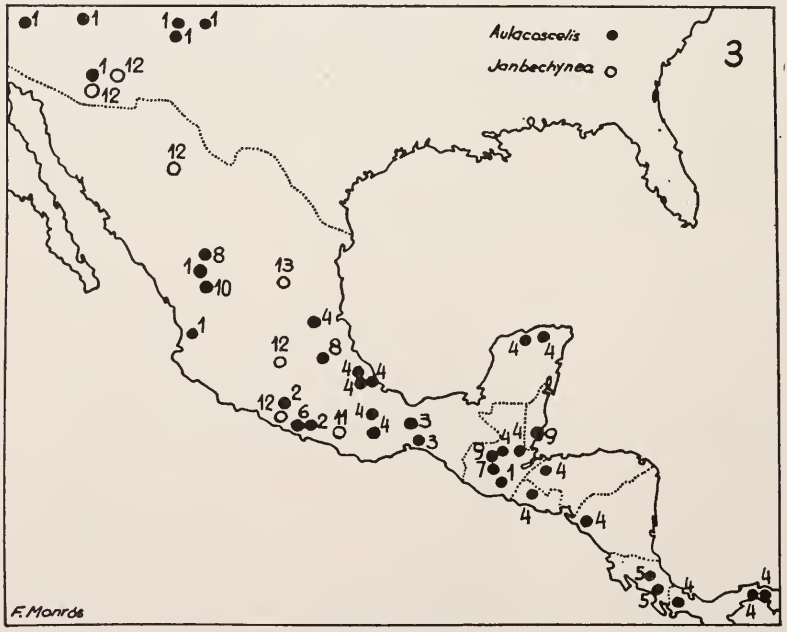
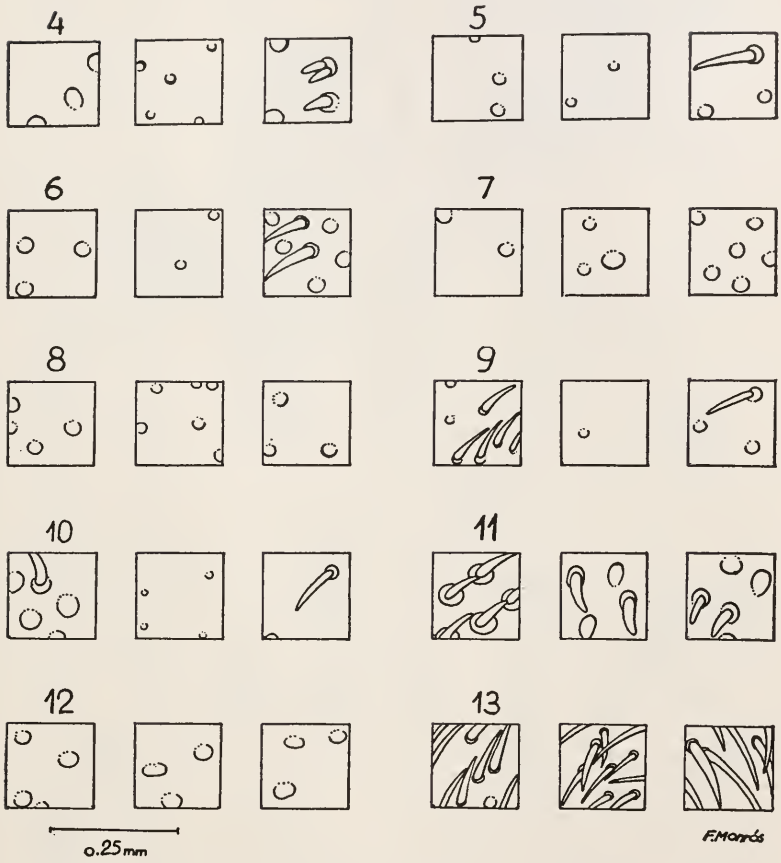


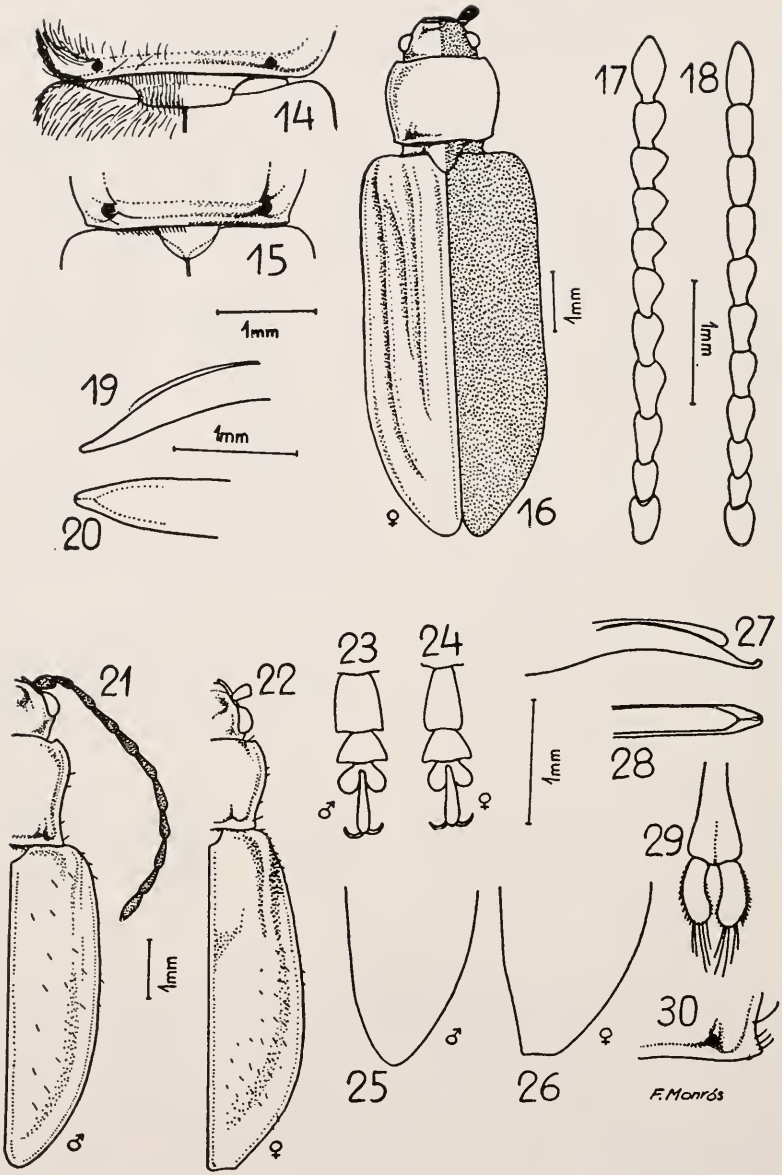
Fig. 1. Phylogenetic relationship of Aulacoscelinae: 1. *Aulacoscelis candezei* Chap.; 2. *A. högei* Jac.; 3. *A. confusa* n. sp.; 4. *A. melanocera* Dup. & Chevr.; 5. *A. costaricensis* Bech.; 6. *A. sanguinea* Jac.; 7. *A. melanocephala* Jac.; 8. *A. variabilis* Jac.; 9. *A. tibialis* Jac.; 10. *A. grandis* Jac.; 11. *Janbechynea* (*Bothroscelis*) *melyroides* (Crowson); 12. *J.* (*B.*) *fulvipes* (Jac.); 13. *J.* (*s. str.*) *elongata* (Jac.); 14. *J.* (*s. str.*) *inverosimilis* n. sp.; 15. *J.* (*s. str.*) *paradoxa* Monrós.

Fig. 2. General distribution of Aulacoscelinae.

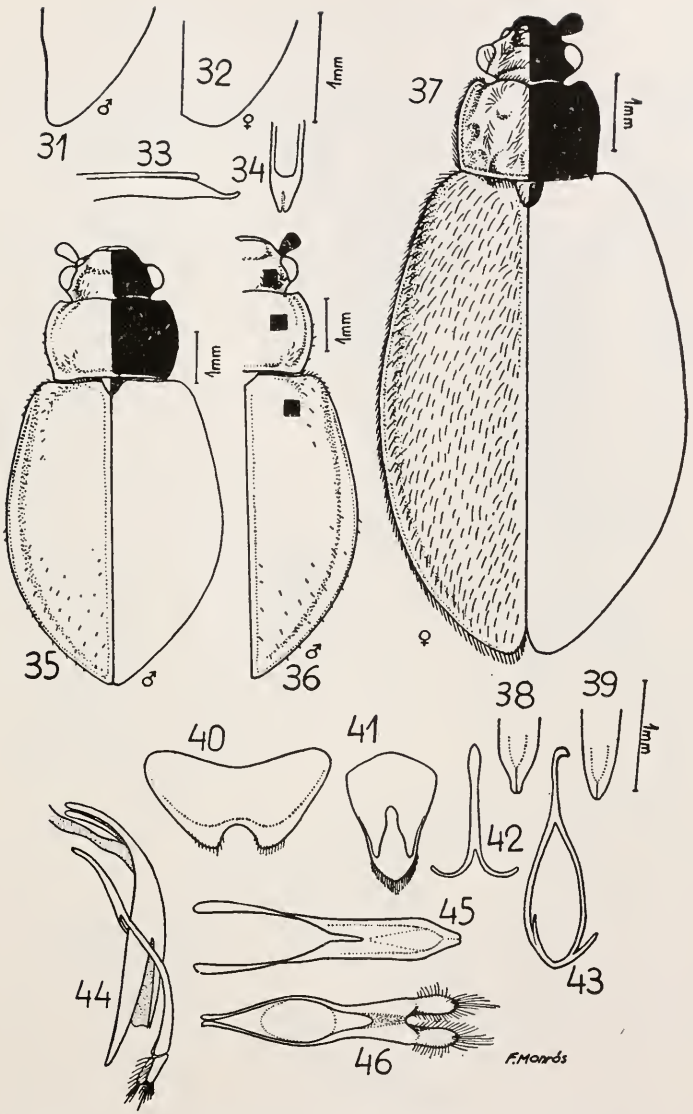
Fig. 3. Distribution of the Central American species of Aulacoscelinae; numbers as in Figure 1.



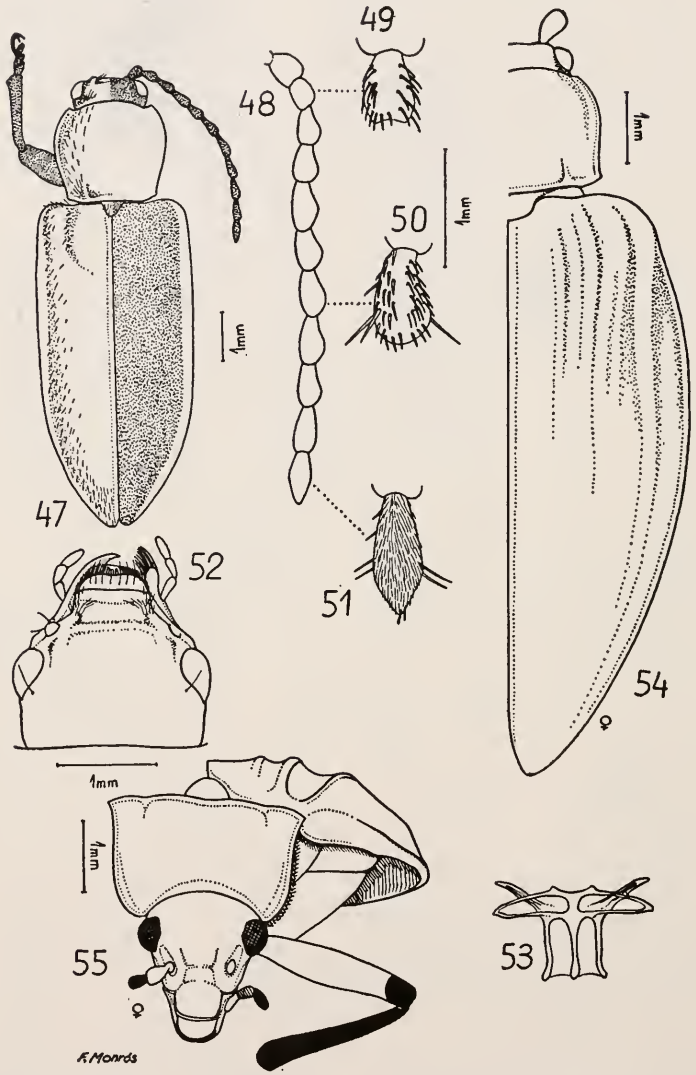
Figs. 4-13. Dorsal punctures and pilosity in *Aulacoscelis*. In each case the left square is taken from the head, the central square from the prothorax, and the right square from the elytra; the places indicated by the squares are represented in Figure 36. The microsculpture is not indicated in the figures. 4. *A. candezei* Chap.; 5. *A. högei* Jac. 6. *A. confusa* n. sp.; 7. *A. melanocera* Dup. & Chevr.; 8. *A. costaricensis* Bech.; 9. *A. sanguinea* Jac.; 10. *A. melanocephala* Jac.; 11. *A. variabilis* Jac.; 12. *A. tibialis* Jac.; 13. *A. grandis* Jac.



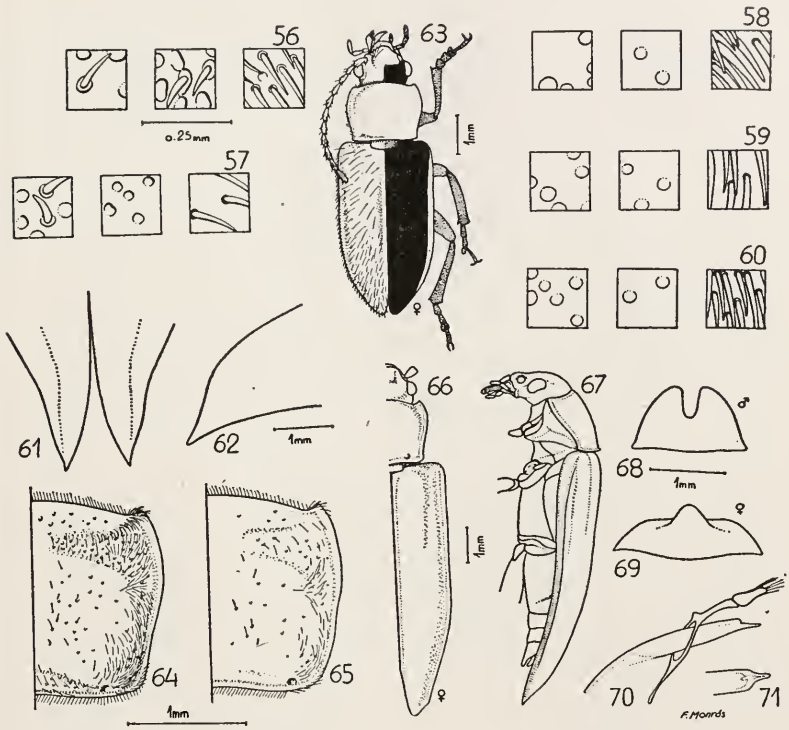
Figs 14-30. 14. Base of prothorax, scutellum and base of elytra in *Janbechynea* (*Bothroscelis*) *fulvipes* (Jac.). The pilosity indicated on the left side, only the structure on the right side. 15. Same in *Aulacoscelis melanocera* Dup. & Chevr. 16. *Aulacoscelis candezei* Chap. The specimen illustrated is a paratype of *A. purpurea* Horn in PAS; structure indicated on left side, color on right side. 17. Antenna of *A. högei* Jac. cotype ♂ (pilosity not indicated). 18. Same of *A. confusa* n. sp. holotype ♂. 19. Male genitalia of *A. högei* Jac.; apex of median lobe from the side. 20. Same from below. 21. *Aulacoscelis costaricensis* Bech. ♂ topotype in USNM. 22. Same, ♀. 23. Same, anterior tarsi of ♂. 24. Same, of ♀. 25. Same, apex of elytron of ♂. 26. Same, of ♀. 27. Same, ♂ genitalia, from the side. 28. Same, from above. 29. Same, median dorsal process of tegmen from above. 30. Same, posterior prothoracic angle showing basal fold and groove.



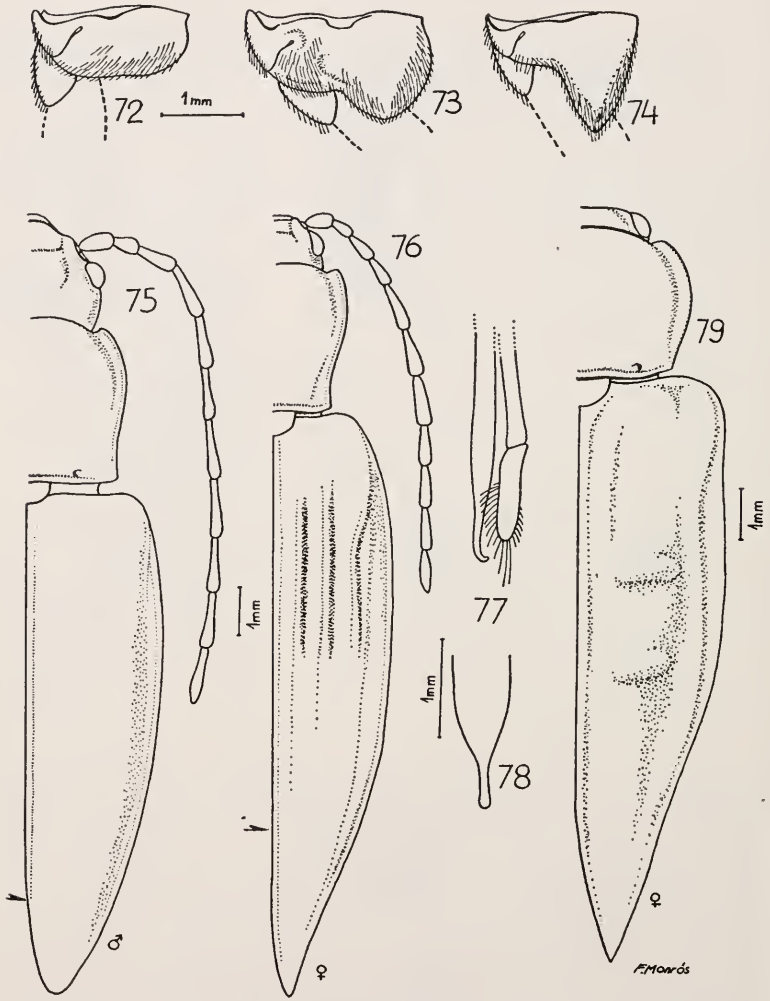
Figs. 31-46. 31. *A. melanocera* Dup. & Chevr.; apex of elytron of ♂. 32. Same, ♀. 33. Same, ♂ genitalia from the side. 34. Same, from above. 35. *A. melanocephala* Jac. holotype ♂ in MCZ; pilosity and structure on left side, colors on right. 36. *A. sanguinea* Jac. cotype ♂ in MCZ; the squares represent the approximate places from which the samples of punctures and pilosity are taken. 37. *A. grandis* Jac. cotype ♀ in MCZ (as fig. 35). 38. *A. melanocephala* Jac. ♂ genitalia. 39. *A. sanguinea* Jac. ♂ genitalia. 40. Last sternite of *A. variabilis* Jac., inner side. 41. *A. variabilis* Jac., first invaginated abdominal sclerite. 42-43. Sclerites appended to genitalia ♂ in *A. variabilis* Jac. 44. *A. variabilis* Jac., ♂ genitalia from the side with tegmen and internal sac in place. 45. *A. variabilis* Jac., median lobe of ♂ genitalia from below. 46. *A. variabilis* Jac., annular tegmen from above.



Figs. 47-55. 47. *A. variabilis* Jac. ♀ cotype in USNM (as fig. 35). 48. Same, antenna without pilosity. 49-51. Same, type of antennal pilosity. 52. Same, head of ♂. 53. Same, metendosternite. 54. *A. tibialis* Jac. cotype ♀ in MCZ. 55. Same from front with indication of colors.



Figs. 56-71. 56-60. Dorsal punctures and pilosity in *Janbechynea*. As figs. 4-13. 56. *J.* (*Bothroscelis*) *fulvipes* (Jac.); 57. *J.* (*B.*) *melyroides* (Crowson); 58. *J.* (*J.*) *elongata* (Jac.); 59. *J.* (*J.*) *inverosimilis* n. sp. 60. *J.* (*J.*) *paradoxa* Monrós. 61. *J. inverosimilis* n. sp. apices of elytra. 62. Same, from the side. 63. *J.* (*B.*) *melyroides* (Crowson) paratype ♀ in col. Monrós; as fig. 35. 64. *J.* (*B.*) *fulvipes* (Jac.), pronotal punctures and pilosity in cotype ♂. 65. Same as shown in cotype ♂ of *Aulacoscelis femorata* in MCZ. 66. *J.* (*B.*) *fulvipes* (Jac.). The specimen illustrated is a paratype ♀ of *Aulacoscelis ventralis* Schaeffer in USNM. 67. Same, from the side. 68. Same, last sternite in ♂. 69. Same in ♀. 70. Same, ♂ genitalia from the side. 71. Same, apex of median lobe from below.



Figs. 72-79. 72-74. Metacoxae ♀ from the inner side in *Janbechynea s. str.;* position of femur indicated by dotted lines. 72. *J.* (*J.*) *elongata* (Jac.). 73. *J.* (*J.*) *inverosimilis* n. sp. 74. *J.* (*J.*) *paradoxa* Monrós. 75. *Janbechynea* (*s. str.*) *elongata* (Jac.); the arrow indicates length of abdomen. 76. Same, allotype ♀ in USNM. 77. Same, genitalia ♂ from the side. 78. Same from above. 79. *J.* (*J.*) *inverosimilis* n. sp. holotype ♀ in MCZ (colors and pilosity not indicated).

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 112, No. 5

THE COMPARATIVE BIOLOGY OF REPRODUCTION IN THE WOOD-BORING ISOPOD CRUSTACEAN *LIMNORIA*

By Robert J. Menzies

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

December, 1954

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 112.

Breviora (octavo) 1952 — No. 40 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 33 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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No. 5 — *The Comparative Biology of Reproduction in the Wood-Boring Isopod Crustacean Limnoria*[1]

BY ROBERT J. MENZIES

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1 Contribution from the Scripps Institution of Oceanography, new series, 740. These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of California, S.I.O., NR 163-084.

INTRODUCTION

A study of the biology of an organism necessarily involves the accumulation of data concerning many aspects of its anatomy and behavior. Knowledge about the way in which an animal reproduces, maintaining itself in its environment, is highly significant to an understanding of its biology. Here the external and internal anatomy of the marine pest *Limnoria* is described. Comparisons are made with other isopods in order that an idea may be had of the basic similarities and differences which *Limnoria* shows with the members of the crustacean order to which it belongs. Where possible, correlations are drawn between the structure of the reproductive system and the reproductive behavior of the animal.

This paper represents the results of part of a general study on the biology of *Limnoria* which was done under contract with the Office of Naval Research at the Scripps Institution of Oceanography in the Division of Marine Invertebrates in collaboration with Dr. Martin W. Johnson.

The first study of the internal anatomy of *Limnoria* was made by P. P. C. Hoek (1893, 97 pp., 7 pls.). Although written in Dutch and thus largely unavailable to American scientists, his work represents a most comprehensive study which has often been quoted and which forms the basis for a similar report by Kofoid and Miller (1927, pp. 306-332). Both investigations dealt with the entire organism, with only brief reference to the reproductive system. Various aspects of the reproductive behavior of *Limnoria* are also mentioned briefly by Coker (1923, pp. 95-100), Henderson (1924, p. 320), Johnson (1935, p. 428), Sømme (1940, p. 155) and Shiino (1950, p. 348), all of whom were mainly interested in the ecology of the animal.

MATERIALS AND METHODS

The species investigated was *Limnoria tripunctata* Menzies (Menzies, 1951, pp. 86-88) collected from San Diego harbor, California. Its reproductive system has been compared with those of *L. quadripunctata* Holthuis and *L. lignorum* (Rathke). No structural deviations of major importance were found, and it is therefore believed that the findings reported here are applicable to the majority of the species.

Living specimens, whole and decapitated, were fixed prior to sectioning, in formalin (10 per cent), Carnoy's fluid acid alcohol, formalin-alcohol-acetic acid (F.A.A.), and 70 per cent alcohol. Cytological details were best preserved in decapitated specimens fixed in F.A.A. Sections were made of paraffine-embedded samples at 7 μ and 10 μ. Three staining techniques were employed: Heidenhain's iron hematoxylin (counterstain eosin), Mallory's triple stain, and Harris' hematoxylin. The first gave the most generally useful results for this study.

COMPARATIVE MORPHOLOGY OF THE REPRODUCTIVE ORGANS

In common with all known isopods the body of *Limnoria* can be divided into three major regions (Fig. 1): the cephalon or head bearing the eyes, antennae, and mouth parts; the peraeon

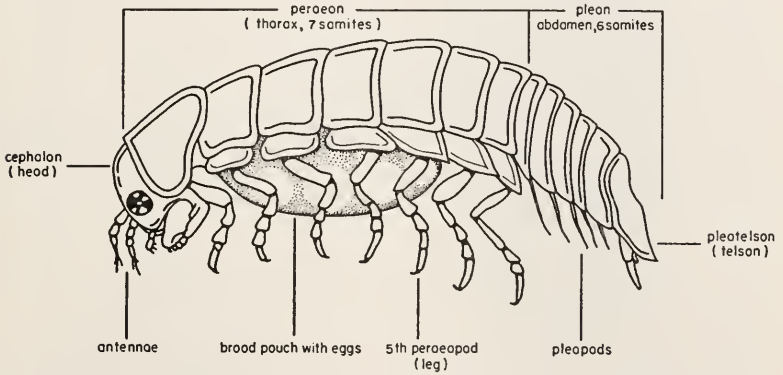


Fig. 1. Gravid female *Limnoria* (from G. O. Sars, 1897). Major regions of the body mentioned in text are noted. (The assistance of Mr. Robert Winsett, Scientific Illustrator, Publications Division, S.I.O., in the final preparation of Figures 1, 2, 5, 6 is particularly appreciated.)

or thorax bearing usually seven pairs of walking legs; and the pleon or abdomen bearing usually five pairs of swimming and respiratory appendages, the pleopods. The male and female gonads are contained within the peraeon. Their relationship to other major organs is shown in Figure 2. In *Limnoria* the sexes are separate but this is not true for several other isopods (p. 372). The body of an adult *Limnoria tripunctata* is roughly 2.50 mm. long and 0.60 mm. wide at the pleotelson.

Internal Anatomy

Female. The ovaries are paired organs located below and on either side of the tubular heart and above the intestine and digestive glands. Each ovary when mature extends from the second to the seventh (last) peraeonal somite. Both their size and extent are governed by the size and number of the developing ova. The

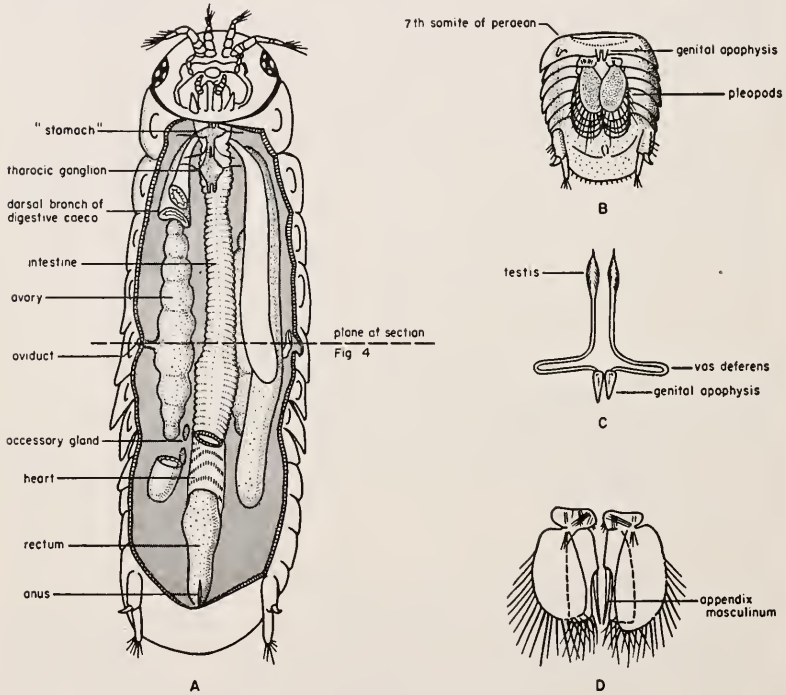


Fig. 2. Internal and external reproductive organs of *Limnoria*. A. Female, ventral view, body wall cut away. B. Male, pleon and seventh somite of peraeon, ventral view. C. Testes. D. Second pleopods of male. Figures B and D after G. O. Sars, 1897; A and C original.

immature ova (Fig. 3C) are about 0.045 mm. along the long axis and have a characteristic uniform cytoplasm when preserved, and a discrete nucleus. Yolk globules are not differentiated. In contrast, the mature ova (Fig. 4) are large oblong yolk-filled cells with a length of 0.30 mm. and a cross-sectional diameter of 0.12

to 0.18 mm. The space occupied by the eggs at the middle of the body is equal to about 30-40 per cent of that of the expanded body cavity itself. The increased volume of the maturing eggs compresses the other internal organs to the extent that females in the stage prior to egg deposition frequently do not have food in the gut.

The oviduct, attached laterally to each ovary at about its middle, extends ventro-laterally to open at the base of the fifth pair of legs. Each oviduct is band-shaped with a length of 0.08 mm., a thickness of 0.01 mm., and a height (distance between ovary and orifice of oviduct) of 0.12 mm.

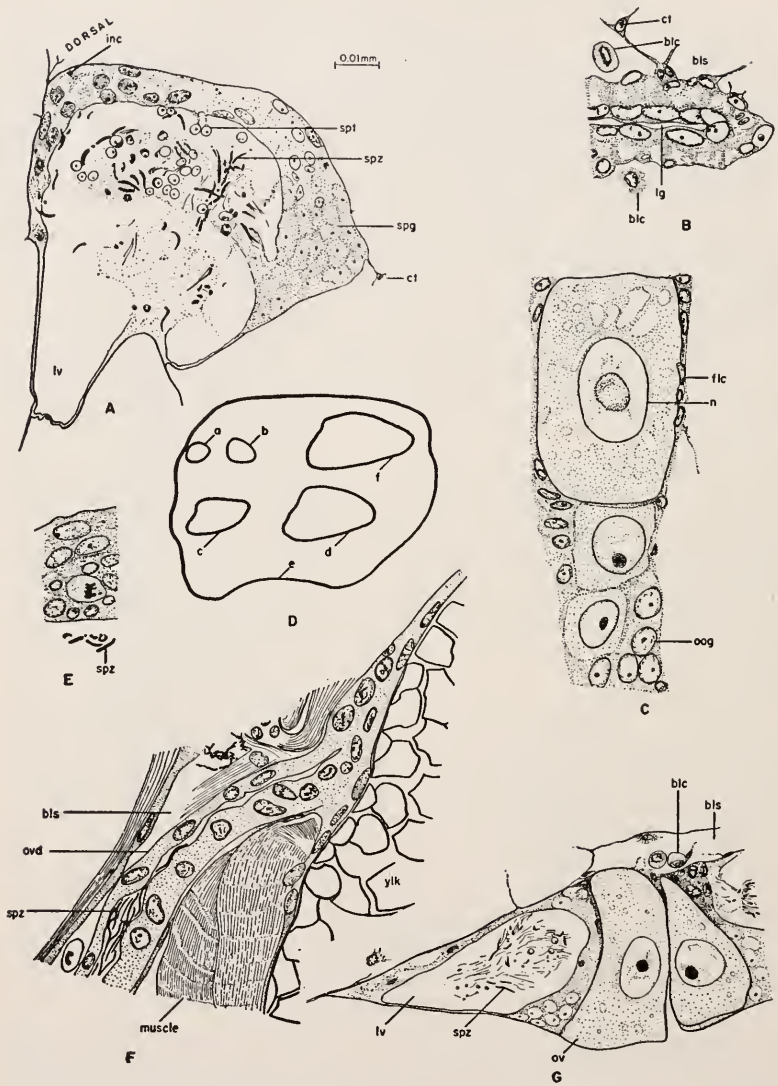
Much of the tissue surrounding each ovum consists of follicle cells (*flc*, Fig. 3C). The oogonia are distributed along the lateral margin of each maturing ovum and at the ends of the ovary (*oog*, Fig. 3C).

Posterior to each ovary are located two elongate glands which have a narrow lumen (called accessory glands by Kofoid and Miller). The function of these is not known. Dorsally they are in contact with the pericardium. Their cells (Fig. 3B) are unlike those of the ovary or any other organ in *Limnoria*. The location of the accessory glands near the heart and their presence only in the female suggest that they might have an endocrine function.

Male. The testes of the male are similarly paired (Figs. 2C, 3A). Each testis consists of a single lobe of approximately 0.08 mm. in diameter and 0.1 mm. in length, located between the fourth and fifth peraeonal somites, below and on either side of the heart and not in the last (7th) peraeonal somite as maintained by Kofoid and Miller (1927, *op cit.*).[1] A vas deferens proceeds from the testis to the seventh peraeonal somite. Here, as is usual for isopods, it turns medially and extends along the ventral body wall to one of the paired genital apophyses. The genital apophyses (=penis) consists of a pair of movable skin folds on either side of the midline of the seventh peraeonal somite.

The structure of the testis is unusual in having only a single lobe. Cytologically, spermatogenesis and spermiogenesis (Fig. 3A) are easily traced. Spermatogonia consist of rectangular shaped cells of uniform consistency and with an evident nucleo-

1 Kofoid and Miller's error might be due to the mistranslation of Hoek's (*op. cit.*, p. 33) statement that the testes were located in the last body segments: "De testes nemen in de laatste borstsegmenten . . ."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lus. Primary spermatocytes have a greatly swollen nucleus and at the metaphase show tightly compacted tetrads and evident centrosomes. The nuclei of secondary spermatocytes are about one-half the size of those of primaries and have peripheral chromatin granules and an evident nucleolus. Spermatids show a variety of structure during their maturation to sperms. The nuclei of early spermatids have a granular nucleoplasm and apparently two nucleoli. Those in a later stage are much smaller with a clear nucleoplasm and two marked nucleoli. Mature sperm have a cap (head?), an elongate midpiece, and a tail piece which is at least twice the length of the midpiece. The precise length of the sperm tail was not determined. Various parts of the testis appeared to be in different phases of development. Morphologically mature sperm, however, were found in the lumen throughout the length of the testis. A hyaline membrane covered the testis and formed the wall of the vasa deferentia. It was associated with minute nuclei of the connective tissue outside the testis and appeared to have been secreted by those cells. Some small nuclei found inside the testis are considered to belong to interstitial cells.

It is common among isopods for sperm to mature together in compact batches (spermatophores). This bunching of sperm was not observed, however, to occur in *Limnoria,* and no spermatophore seems to be produced. Except for this deviation, the

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Fig. 3. Sections of reproductive organs of *Limnoria* A-C, E-F. A. Cross section through testis. B. Longitudinal section through part of an ovarian accessory organ. C. Longitudinal section through immature ovary. E. Part of a cross section through testis showing large primary spermatocytes and smaller secondary spermatocytes. F. Section through oviduct of fertilized female; note sperm in oviduct. *Abbreviations: blc,* bloodcell; *bls,* blood sinus; *ct,* connective tissue; *inc,* interstitial cell; *flc,* follicle cell; *lg,* lumen of accessory gland; *lv,* lumen of vas deferens; *n,* nucleus; *oog,* oogonium; *ov,* ovum; *ovd,* oviduct; *spg,* spermatogonia; *spt,* spermatid; *spz,* spermatozoa; *ylk,* yolk.

D. Outlines of second pair oostegites of *L. quadripunctata,* all drawn to same scale. Widths of pleotelsons of specimens in millimeters are: *a,* 0.59, *b,* 0.65, *c,* 0.70, *d,* 0.77, *e,* 0.77, *f,* 0.88.

Sections all drawn to about the same scale as indicated in figure A; all drawings were done with the aid of a camera lucida.

testis cytologically appeared much like those described for other isopods.

A sperm storage organ or seminal receptacle has been discovered in many of the female isopods whose internal anatomy has been studied. This includes *Trichoniscus, Asellus,* and *Jaera* (Fig. 5). In *Jaera* and *Asellus* the seminal receptacle consists only of a swollen part of the oviduct, but in *Trichoniscus* a separate pouch is present. The genus *Jaera* shows an apparently unusual modification in also having a dorsally-opening vagina. Female *Limnoria* appear to lack any sperm storage organs and in this regard are apparently similar to *Sphaeroma.*

External Anatomy

The secondary sex characteristics of the female consist of leaf-like plates (oostegites) originating at the medial base of the coxal plate of legs two, three, four, and five; and of the paired openings of the oviducts medial to the base of each fifth leg. With the absence of a vagina in the genus, each of these openings might be considered a vulva. The vulvae were not found in immature females. Similarly the oviducts seemed to remain closed (without a lumen) until a short time prior to copulation.

The male secondary sex characteristics consist of the genital apophyses (Figs. 2C, 6) which were already mentioned and a stylus-like appendage (appendix masculinum) attached on the medial side of the endopod of each second pleopod (Fig. 2D).

The secondary sex characteristics of isopods show some remarkable variation. For example, oostegites do not appear in the suborder Gnathiidea (Monod, 1926, pp. 202-210), Fig. 5E, although the area of the ventral part of the body surrounding the genital atrium might be considered homologous. Oostegites, as indicated for *Limnoria,* are present in most members of the suborders, e.g. Anthuroidea, Flabellifera, Bopyroidea, Valvifera, Asellota and Oniscoidea. The movable plates which form the genital apophyses of *Limnoria* develop from simple swellings of the integument. Such swellings constitute the adult condition in *Cymothoa* (Fig. 6G). A fusion of these lobes into a single piece (ductus ejactulatorius) seems to have occurred in at least two suborders independently. Thus *Idothea* (Valvifera) has two plates, whereas *Synidotea* has one (Valvifera). *Ligidium* has two, while *Philoscia*

(Fig. 6C) has one (Oniscoidea). An appendix masculinum is present on the endopod of the second pleopods of males belonging to the suborder Flabellifera. Here its function is not known but it has been presumed to act as an intromittent organ in passing the sperm from the genital apophyses to the vulva (or equivalent opening) of the female. In the suborder Asellota (the genus *Asellus* perhaps being exceptional), the first two male pleopods combine as a functional penis. This is the case also in the suborder Oniscoidea (Vandel, 1925); however, the pleopods are of a structure quite different from those of the Asellota (Fig. 6D).

Within the suborder Flabellifera, each appendix masculinum consists only of a flattened part of the endopod of the second pleopod which originates by splitting off the endopod. In most genera it is within the realm of possibility that the appendix is long enough to reach the oviducal opening of the female; however, on the appendix masculinum of *Limnoria* the lack of any grooves, specialized bristles, or rugosities, in which sperm might be transferred or held prior to or during copulation, suggests that the appendix masculinum might not have such a function. On the other hand, the genital apophyses are generally so short and located so near the midline of the male that it is difficult to imagine that these might reach the vulvae of the female which in contrast are located at the base of the legs of the female, far from the midline. Copulation among the Flabellifera has not been observed in detail and, therefore, no solution to the above puzzle is offered.

SEX DETERMINATION

Sex Ratio

The sexes of *Limnoria* are found in about a 50/50 ratio when taken from piling populations (Station A,[1] mean ratio of males to mature females, 0.95, and Station B,[2] mean ratio of males to mature females, 1.06; see Table 1). It is probable that males and females are produced in that ratio; however, this needs further confirmation. The presence of sex chromosomes might be suggested for *Limnoria* and other marine isopods in view of the finding by Staiger and Bocquet (1954) of female heterogamety in the marine isopod *Jaera marina*.

1 Located at the U.S. Navy Target Repair Base, Point Loma.
2 Located near the San Diego landing of the Coronado Ferry.

TABLE 1

Ratio of males to females (those with oostegites) on piling. Specimens were taken from heavily infested wood, each sample averaging about 1 square inch in area.

Month	Station A	Station B
September 1952	0.95	0.83
October 1952	1.05	1.19
November 1952	1.26	0.93
December 1952	1.26	—
January 1953	1.12	1.31
February 1953	0.65	1.00
March 1953	1.20	1.00
April 1953	0.44	1.19
May 1953	0.95	—
June 1953	1.00	—
July 1953	1.92	—
August 1953	0.65	—
Mean	0.95	1.06
Mean Sta. A and B	0.99	

Ambisexual Individuals

Ambisexual animals, those having the primary and secondary characteristics of both sexes, were encountered rarely. Out of the 1423 sexually mature animals examined from thirteen migrant populations, they were found only twice; once in a sample having 39 specimens, and once in a sample having 137 specimens. Three were found out of a total of 657 specimens from piling; one sample of 91 animals had two while another of 30 animals had one. These individuals had the genital apophyses of the male as well as the immature or postgravid oostegites of the female.

Sections of one ambisexual individual (Fig. 3G) showed the presence of ovaries with immature ova as well as testes with mature sperm. No oviducts were found. Protandry is a characteristic feature of one family of the Flabellifera, the Cymothoidae, in which the young are functional males (with rudiments of ovarian tissue) and progressively become functional females. In the Sphaeromidae, rudimentary testes are attached to the ovaries of the female.

REPRODUCTIVE BEHAVIOR

Brood-Pouch Formation

The development of the oostegites prior to copulation and brood deposition is a gradual process with their size increasing as the animal grows (Fig. 3D). Copulation, fertilization, the production of the large oostegites of the fully formed brood pouch, and egg deposition into the pouch of *Limnoria* all appear to take place within a brief period of time (probably no more than two or three days). The release of the young from the brood pouch is followed by a molt of the female (several laboratory observations) and a reduction in size of the oostegites to their pregravid size (Fig. 3D). This was suspected earlier to be the case when females with small oostegites were found to have apparently recently released young in their burrows. It follows then that females with pregravid oostegites can be either virgin

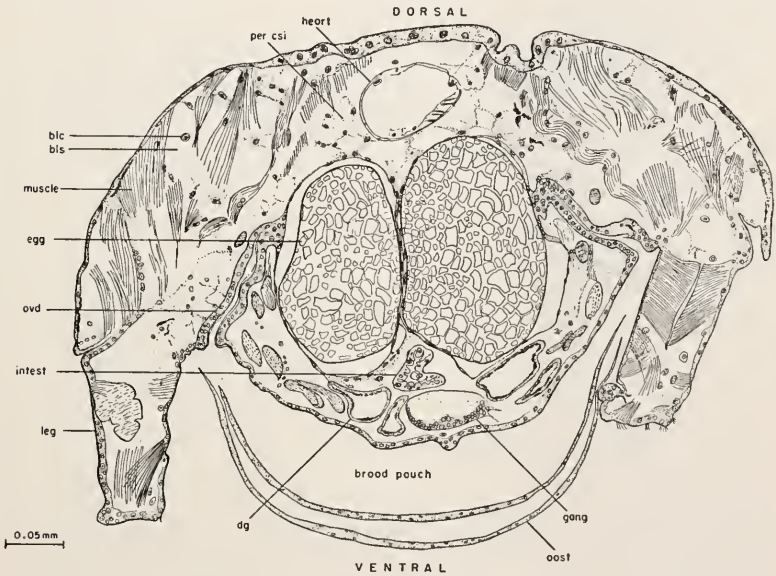

Fig. 4. Cross section through pre-gravid female *Limnoria* at oviduct. The animal had molted and the chitin was not heavily sclerotized at this stage. Note huge size of eggs and absence of food in intestine. Abbreviations, same as for Figure 3 with the following added: *dg,* digestive gland; *gang,* ganglion; *intest,* intestine; *oost,* oostegite; *per csi,* pericardial sinus.

females or females which have already produced one or more broods.

Incubation

Limnoria incubates its young within its external brood pouch (Fig. 5B). This mode of incubation is common to the majority of isopods, including the suborders Asellota, Oniscoidea, Valvifera, Anthuridea, Bopyroidea, Phreatoicidea, and most of the

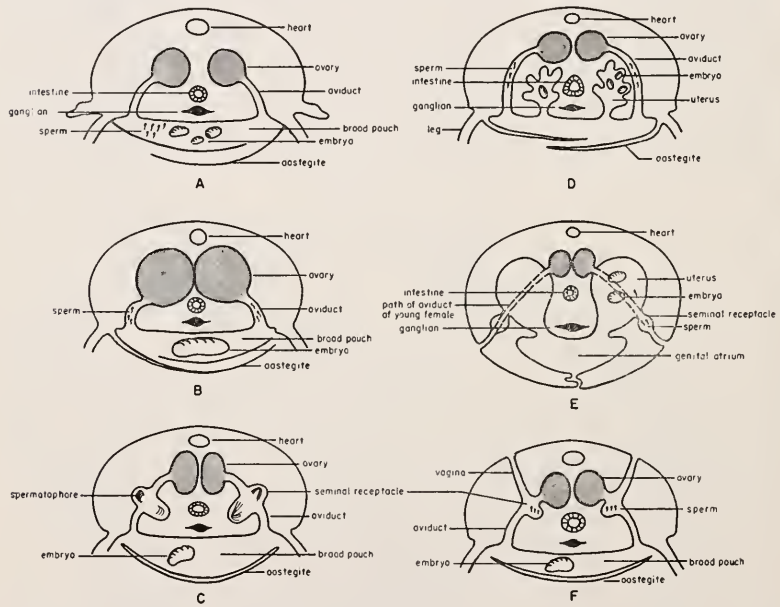

Fig. 5. Schematic diagrams of the female reproductive systems of the Isopoda. A. *Epipenaeon*, note external fertilization and absence of sperm storage organs. B. *Limnoria*, note absence of sperm storage organs. C. Oniscoid isopods, note presence of seminal receptacle and/or spermatophores. D. *Sphaeroma*, note presence of uterus and functionless "brood pouch." E. Adult *Paragnathia*, note absence of brood pouch and modifications undergone by female in development. F. *Jaera*, note presence of dorsal vagina. Figure A based on data from Hiraiwa (1936); B, original; C, from Vandel (1925); D, from Leichmann (1891-93); E, from Monod (1926), young based on figures given by Monod, adult from description by Monod; F, from Forsman (1944).

Flabellifera. The Gnathiidea and the Sphaeromidae (suborder Flabellifera) incubate their young "internally." In the Sphaeromidae the eggs are deposited into the brood pouch but then are taken into uteri which consist of paired invaginations of the ventral body wall. In the Gnathiidea no brood pouch is formed; instead the eggs are deposited into a genital atrium and then taken into the uteri which are reminiscent of those of the Sphaeromidae.

Pairing, Fertilization, and Burrow Construction

The occupation of a burrow usually by only a sexually mature male and female (plus any young produced by the pair) has been

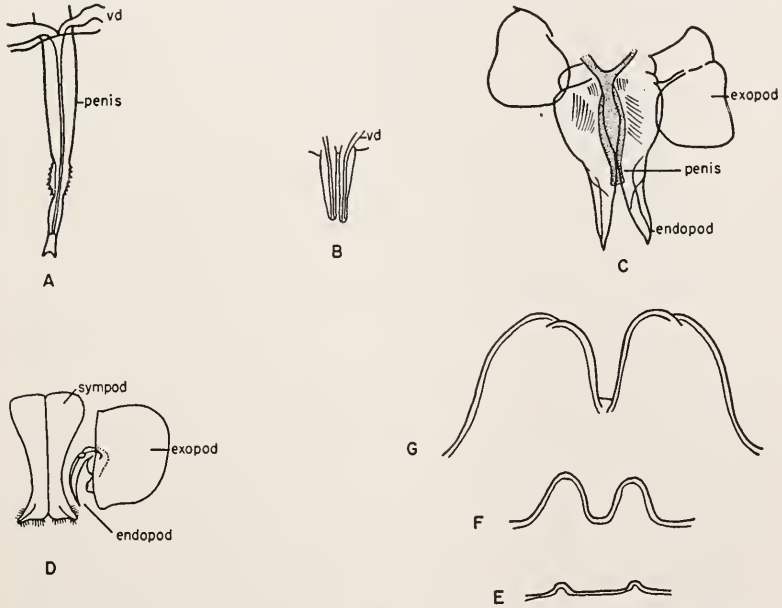

Fig. 6. Male reproductive organs. A. Penis of *Trichnoiscus dentiger* (after Vandel, 1925), B. Genital apophyses of *Ligidium hypnorum* (after Vandel, 1925), C. First pleopods and penis of *Philoscia muscorum* (after Vandel, 1925), D. First two pleopods of *Ianiropsis* sp. (after Menzies, 1952), E-G. Genital apophyses, E. Adult *Cirolana*, F. Young *Limnoria*, G. Adult *Cymothoa*, all original. Scales of magnification variable. Abbreviations same as for other figures, *vd*, vas deferens.

TABLE 2

A comparison of the length of burrows occupied by single or by paired animals on test blocks of one- and two-month exposure at the U.S. Naval Target Repair Base, San Diego harbor, California (1953).

Burrow Length in mm.	No. Burrows with Single Animals		No. Burrows with Paired Animals	
	One-Month	Two-Month	One-Month	Two-Month
1.5	3	3	0	0
3.5	42	13	2	0
5.5	11	10	16	2
7.5	1*	6	12	8
9.5		1*	24	16
11.5			2*	14
13.5				10
15.5				9
17.5				2
19.5				1
21.5				1
23.5				1*
Total	57	33	56	64
Mean Burrow Length	3.8±0.97	4.8±1.95	7.6±1.9	11.8±3.4

* Length of longest burrow.

frequently observed (Henderson [1924], Johnson [1935], Shiino [1950], etc.). Examination of burrows in test blocks revealed that a burrow generally had two animals only when long enough to fully enclose two specimens (around 5.5 mm. and longer). The proportion of paired animals was found to increase markedly as the length of burrows and the length of exposure to migrant populations increased. Test blocks of one-month exposure had about as many burrows occupied by one as occupied by two animals, while those of two-month exposure had twice as many paired organisms as single ones (Table 2). Organisms kept in the laboratory have been observed to pair with each other for periods exceeding ten months (one case) and four months (four cases); presumably a similar relationship between paired sexes can be expected to occur in nature. Accordingly, it appears

that the pairing of sexually mature animals within a burrow is an essential and consistent feature of their biology.

Copulation apparently occurs in the burrow. The sperm produced by the male are relatively few in number and these, as has been seen, are not combined into a spermatophore. Sperm have been found in the oviduct of the female and probably fertilize the eggs as they pass down the oviducts. The absence in the female of any seminal receptacle suggests that a copulation must precede the deposition of each brood. This is more strongly indicated by the observation that sperm were not found in the oviducts of females bearing embryos or in virgin or post-oviger-ous females but only in those with ripe ovaries which were molting, prior to egg deposition (Fig. 3F). In the terrestrial isopods which have been extensively studied in this regard and which bear a seminal receptacle, a single copulation has been found sufficient for the production of two broods (*Armadillidium*, Howard, 1940, p. 84). Heeley (1941, pp. 136-137) reports viable sperm to have been stored by isolated females of *Porcellio dilatatus, P. scaber* and *Oniscus asellus* for at least two successive year's brood. The sexes of *Porcellio* and *Armadillidium* show no tendency to pair and in the case of the latter, natural populations often have twice as many of one sex as the other (Howard, *op. cit.*). Oniscoid isopods (*Porcellio, Trichoniscus, Armadillidium,* etc.) usually have a seminal receptacle and the males produce many sperm which are united into a spermatophore (Schöbl, 1880; Vandel, 1925). In contrast, it is interesting to note that the diverse genera in which a long-term sexual pairing is a pronounced characteristic of the animals, no seminal receptacle is known to exist. These include the bopyrid, *Epipenaeon,* in which fertilization is apparently external (Hiraiwa, 1936, p. 108), the commensal and parasitic cymothoid, *Anilocra physoides* (Montalenti, 1941, pl. XIX), and *Sphaeroma* (Leichmann, 1891). It appears that pairing, a long-term association of members of the opposite sex, is correlated generally with an absence of sperm storage organs in the species which have been studied. In *Limnoria,* in view of its pairing habit, the production of sperm storage organs would teleologically seem superfluous.

There exists the remote possibility that parthenogenesis (which is known for several species of terrestrial isopods) might occur

in *Limnoria*. Five females kept for one year without a male failed to produce any brood, whereas seven paired animals produced one to two broods during that time. Hence parthenogenesis by *Limnoria* is considered unlikely.

TABLE 3

Size of broods (egg number) produced by various isopods

Classification	Species	Reference	Brood Size
ONISCOIDEA			
Ligiidae	*Ligia oceanica*	Vandel, 1925	25
	Ligidium hypnorum	" "	3-17
Trichonisidae	*Trichoniscus provisorius*	" "	3-19 (7-11 av.)
	Trichoniscus flavis	" "	6-18 (12 av.)
Oniscidae	*Tracheoniscus rathkei*	" "	63
	Porcellio monticola	" "	73
	Porcellio scaber	" "	88
	Oniscus asellus	" "	74
Armadillidiidae	*Armadillidium vulgare*	" "	up to 200
FLABELLIFERA			
Cymothoidae	*Anilocra physodes*	Legrand, 1952	100-350
	Livoneca convexa	Original	67-130
Limnoriidae	*Limnoria* spp. (4)	This paper, p. 380	1-32 (6-21 av.)
Sphaeromidae	*Sphaeroma rugicauda*	Leichmann, 1891-93	63
GNATHIIDEA			
	Paragnathia formica	Monod, 1926	100+ (in ovary)
ASELLOTA			
Janiridae	*Jaera albifrons*	Forsman, 1944	5-60
	Desmosoma spp. (3)	Hult, 1941	8, 12, 16 (av.)
	Ilyarachna sp.	" "	64
Munnopsidae	*Munnopsis typica*	" "	32 (greatest number)
ANTHURIDEA	No data available		
BOPYROIDEA			2000+ ("several
Bopyridae	*Epipenaeon*	Hiraiwa, 1936	thousand")
VALVIFERA			
Idotheidae	*Idothea (P.) resecata*	Original	46 (29-65)

Size of Brood

The size of the broods produced by *Limnoria* is comparatively small and variable both with regards to species and differing populations of the same species.

Isopods with pelagic young (bopyrid parasites) characteristically produce thousands of eggs per brood (Table 3). Other marine isopods belong to a category of marine organisms which produce fewer than a thousand young per brood (Thorson, 1950, p. 4). No free-living form is known to brood an excess of three hundred eggs.

The members of the genus *Limnoria* produce an average maximum of only 30 eggs per brood. Since few marine animals, even isopods, produce a smaller number of eggs, *Limnoria* may be classified with those marine animals which produce only a few eggs at one time. Except for the correlation between pelagic development of young and a high egg number, which is the rule among marine invertebrates, egg number among the isopods shows no pronounced phylogenetic correlation or pronounced correlation with size. Thus, within the suborder Oniscoidea, egg number per brood varies between 3 and 200, and in the suborder Flabellifera between 32 and 350. The size of the species is not a significant factor governing egg number because *Ligidium hypnorum,* a species much larger than *Limnoria,* does occasionally produce even fewer eggs than *Limnoria.* Similarly cymothoids which are generally much larger than many bopyrids produce several times fewer eggs. The number of eggs produced by an isopod seems more intimately related to the ecology and behavior of the species, and those factors influencing survival rate, than to other factors. One might suspect, in the burrow-producing *Limnoria,* that the survival rate of the young is very high in view of the animal's small brood size.

To judge from the available data on brood size (Table 4), it appears that the different species of *Limnoria* have differing brood sizes. Thus *L. lignorum* has been observed with a maximum of 35 eggs (mean 22), *L. quadripunctata* with 17 eggs at a maximum (9.5 mean), *L. tripunctata* with a maximum of 22 eggs (*ca.* 4-10 on an average), and finally *L. andrewsi* with a maximum of only 6 eggs. Here it is interesting to note that *L. lignorum,* a boreal species, has the greatest number; whereas,

L. andrewsi, a tropical species, has the least.

The evidence thus far assembled does not conclusively suggest, as has been the observed case for many organisms, that younger specimens (smaller) produce fewer eggs than larger specimens. In the species *Limnoria lignorum* (Rathke), Sømme (1940) reported that broods produced during the summer were on an average larger by 10-12 eggs than autumn broods. Coker (1923)

TABLE 4

Number of eggs per brood in several species of *Limnoria*

Species	Kind of Distribution	Reference	Locality	Egg Number Mean	Egg Number Range
L. lignorum (Rathke)	Arctic-Boreal	Henderson (1924)	St. Andrews, Bay of Fundy	21.7	14-32
		Johnson (1935)	Friday Harbor, Washington	—	10-23
		Sømme (1940)			
		a. summer broods	Flødvigen,	20-30	20-35
		b. autumn broods	Nor.		10-20
L. quadri-punctata Holthuis	Temperate	Kofoid and Miller (1927)	San Francisco Bay, Calif.	9.5	1-17
L. tri-punctata Menzies	Temperate	Coker (1923) piling populations	Beaufort, N.C.		
		a. early spring broods		4.2-6.6	1-12
	and	b. summer broods and fall		1.5-4.0	1-9
		c. winter broods		none	none
	Tropical	Shiino (1950) ORIGINAL	Misaki, Japan	—	1-8
		a. piling populations	San Diego, Calif.	4.6±2.74	1-14
		b. Test-block population A	San Diego, Calif.	10.6±3.94	1-18
		c. Test-block population B	San Diego, Calif.	9.6±4.24	1-22
L. andrewsi Calman	Tropical	Shiino (1950)	Kominato, Japan	*ca.* 4-5	2-6

conversely found spring broods larger than summer and fall broods by several eggs (Table 4). He found no gravid females during the winter months. During the spring (April to May) the mean water temperature was near 17°C; during the summer and fall (June to September) it was near 26°C and never below 22°C. In contrast the 5-day averages of the winter water temperatures (December 13 to early March) varied between 11.3°C and 5.2°C. His data strongly suggest a close correlation between temperature and the production of eggs and a less strong correlation between temperature and brood size. Coker probably was working with *tripunctata* (not *L. lignorum*) which is the only species known to occur in North Carolina. As far as is now known *L. lignorum* does not occur south of Massachusetts on the Atlantic Coast.[1]

Sømme (*op. cit.*) found gravid females of *L. lignorum* throughout the year with maximal numbers occurring at temperatures averaging only 9°C and lesser numbers occurring when the temperatures averaged 3.9°C. During periods having similar water temperatures Coker (*op. cit.*) found no gravid females of *L. tripunctata*. Sømme's evidence (*op. cit.*) indicated that little or no egg deposition occurred during the winter months but that the eggs deposited earlier were carried throughout the winter by the female.

These data indicate that an optimal range of temperature for the production of maximal-sized broods might occur in both species.

The presence of gravid females of *L. tripunctata* from piling in San Diego harbor and their absence from test blocks of one-month exposure during the winter months, when the temperature of the water was below 17°C, suggests a similar phenomenon; however, their presence on test blocks of two-months' exposure strongly indicates that egg deposition does not cease entirely as Coker found at Beaufort, but is only retarded under these less extreme conditions (Table 5).

In the case of *L. tripunctata* from San Diego harbor where temperatures near to Beaufort's spring temperatures (17°C) prevailed, it seems that factors besides temperature govern brood size. It has been found that migrant females (those from test

1 Unpublished data.

TABLE 5

Seasonal occurrence of gravid females in piling and test-block samples in San Diego harbor.

Month	Mean Water Temperature (approximate)	Temp. at Collection	Piling		Test-Block				Temperature at Collection
					One-Month Exposure		Two-Month Exposure		
			Per cent Gravid Females	Total Mature Females Examined	Per cent Gravid Females	Total Mature Females Examined	Per cent Gravid Females	Total Mature Females	
September 1952	17-18°C	17.8	52	63	10	78			**17.4
October 1952		18.0	27	22	36	25	33	**33	**18.8
November 1952		16.9	22	37	8	12			**16.9
December 1952		15.1	5	20	*0	21	68	**22	**14.8
January 1953	15°C	14.9	12	25	*0	6			**14.0
February 1953		14.9	25	20	*0	14	72	**22	**15.4
March 1953		15.3	21	19	*8	13			
April 1953		14.1	32	38	*3	34	54	13	
May 1953		16.6	11	19	29	42			
June 1953	17-18°C	18.2	30	47	10	40	67	12	
July 1953		19.7	15	13	7	27			
August 1953		18.6	50	46	41	27	73	15	

* Sum of animals from three blocks, others from one block only.
** Year 1953 to 1954, not 1952 to 1953 as are all others.

blocks) produce an average of 5 more eggs per pouch than nonmigrants (those from piling populations). The variable factor which correlates best here is differences in population density. The mean number of animals per square inch on test blocks of one-month exposure (Station A) from the top and bottom surfaces of the blocks for one year was 3.9.[1] The maximum density encountered (August 13, 1953) on those surfaces was 60 per sq. in. In contrast the density of piling populations (also sampled monthly at Station A) varied between 142 (lowest figure) and 620 (highest figure) animals per square inch (Table 6). A similar relationship between population density and fecundity has been indicated by Park (1939) for the flower beetle *Tribolium confusum*. It is equally difficult in the case of *Limnoria* to prove the *modus operandi* of a population density factor in lowering the fecundity of a population.

The fact that different species have differing brood sizes is of considerable interest indicating that perhaps the ecological factors associated with the reproductive capabilities of the various species are also different. Differences may be found in the frequency with which the broods are produced but this is an item about which no data are available at present.

TABLE 6

Egg number per brood of females from a piling population (presumably nonmigrant) and a test-block population (migrant) compared. Data collected at monthly intervals (1952-53) for twelve-thirteen months in San Diego harbor at two widely separated stations.

Location	Number of Gravid Females Examined	Mean Number of Eggs	σ $\pm$	Range
Piling, Sta. A.	307	4.66	2.70	1-14
Test-block, Sta. A.	105	10.06	3.94	1-18
Test-block, Sta. B.	113	9.63	4.27	1-22

1 An empirically determined ratio of 1.5 animals times the number of burrows has been used here to estimate the total population of each test-block.

DISCUSSION

From this study it is apparent that the reproductive system of *Limnoria,* except for the fact that fertilization is internal, is a simple one with none of the specializations such as a vagina, spermatophore, seminal receptacle, or "internal" uterus which are known for many other isopods. Correlated with this simplicity of structure is the tendency of an adult of each sex to occupy a single burrow for long periods of time. This latter phenomenon suggests that *Limnoria* shows an elementary social life, with the paired animals working together in the construction and maintenance of a burrow and the production of the young.

The observation that the size of the brood of the various species is different, with the more tropical species having a fewer number of eggs than the species living in colder water, suggests that the rate at which broods are produced might be different with the different species. The fact that the rate of production of broods is dependent upon the environment inhabited by a species (as indicated by the data given here and earlier by Coker [1923] and Sømme [1940]) strongly suggests that the rate of brood production is not constant. These observations lead to a method for the evaluation of one hypothesis as to the cause of migration by *Limnoria,* namely overcrowding of the burrows. Once production rates for species in various localities and during various seasons are determined, these may be compared with the migratory picture, and a relationship based on more direct evidence can be established. The data indicate another important item relative to brood production, namely that both high and low temperatures encountered by a species can be associated with a lowering of the brood size. A rising environmental temperature then cannot be presumed always to be accompanied by a corresponding rise in the size of broods or in the rate of brood production.

Perhaps the most significant observation, one which should play a profound role in an estimation of the productivity of natural populations, is that the brood size of specimens from dense piling populations was found to be significantly lower than that of specimens from less dense migrant populations. Investigation of the factors associated with this observation should lead

to a better understanding of the population dynamics of this species as such investigations have done with other organisms for which this phenomenon has been reported.

SUMMARY

1. The internal and external anatomy and general histology of the reproductive organs of *Limnoria tripunctata* Menzies are described and compared with those of other isopods.

2. The male was found to have one-lobed testes in contrast to most isopods and was found not to produce spermatophores.

3. The female was found to have no sperm storage organs. Sperm were observed in the oviducts and it is believed that fertilization of the eggs occurs as they are passed down the oviducts into the brood pouch.

4. The absence of spermatophore production by the male, the absence of sperm storage organs in the female, and the finding of sperm in the female oviduct only prior to egg deposition suggest that a copulation must precede each brood.

5. The method of copulation was not observed. The simple unmodified structure of the appendix masculinum suggests that it is possibly not involved in sperm transfer.

6. A sex ratio of one male to one female is suggested from piling population analysis.

7. Ambisexual individuals were rarely encountered. These individuals had the genital apophyses of the male as well as the oostegites of the female externally and both testes and ovaries internally.

8. It was found that oostegites gradually increase in size until, within one molt, they suddenly increase greatly to form the brood plates of the brood pouch of the gravid female. A release of the young was observed to be accompanied by a molt of the female and a return of the oostegite to a pregravid size. Accordingly, it is indicated that females with pregravid oostegites can be either virgin females or females which have produced one or more broods.

9. The long-term pairing of a sexually mature male and a female in a burrow apparently is an essential and consistent feature of the biology of *Limnoria*. Specimens have been observed to remain paired as long as ten months.

10. The pairing behavior of *Limnoria* and that of several other isopods appears generally to be associated with an absence of any sperm storage mechanism.

11. The reproductive system of both sexes of *Limnoria* is simple in its organization as compared with that of other isopods.

12. Parthenogenesis does not appear to occur in *Limnoria*.

13. *Limnoria* belongs to a category of isopods which produce only a few eggs (average maximum of 30) per brood. A high survival rate of the young and/or a rapid rate of production is indicated.

14. Brood size was found to vary both with regards to the species and differing populations of one species.

15. The boreal species *L. lignorum* (Rathke) produces as many as 35 eggs per brood, whereas the tropical *L. andrewsi* Calman produces only 6 at a maximum. The temperate and temperate-tropical species *L. quadripunctata* Holthuis and *L. tripunctata* Menzies were found to produce broods between those extremes in size.

16. Under conditions of moderately low temperature (near 10°C) at Beaufort, N. C., *L. tripunctata* produced no broods. The brood production of the same species at San Diego during the winter months (temperature near 15°C) was retarded but did not cease entirely.

17. The data suggest that both high and low temperatures are associated with a lowering of brood size in *L. tripunctata* at Beaufort, N. C.

18. At San Diego harbor where seasonal temperature variations are moderate as compared with Beaufort, N. C., variation in brood size was found to correlate with population density, with animals from piling populations (high density) having fewer eggs per brood than animals from test-block populations (low population density).

19. A method of testing the hypothesis that overcrowding is the cause of migration in this species is proposed.

20. The following factors are indicated as important in estimations of the production rate of *Limnoria*: a) species involved, b) temperature and its effect on brood size and rate of brood production within a single species, c) population density and its associated factors as they affect brood size.

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 112, No. 6

THE GENUS *EUSTALA* (ARANEAE, ARGIOPIDAE) IN CENTRAL AMERICA

By Arthur M. Chickering

Albion College, Albion, Michigan

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
March, 1955

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY

AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 113.

Breviora (octavo) 1952 — No. 41 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 34 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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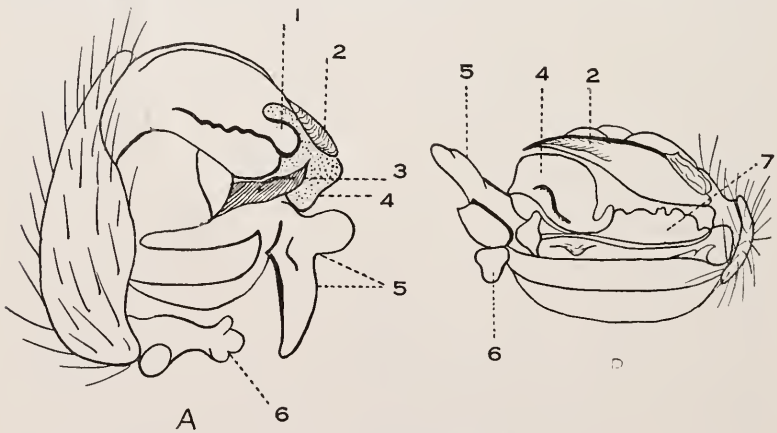
No. 6— *The Genus Eustala (Araneae, Argiopidae) in Central America*

By Arthur M. Chickering

In connection with previous publications (1943, 1948, 1950) I have pointed out some interesting instances of the process of speciation among certain genera of spiders in Panama. The present study of the genus *Eustala* has been somewhat broadened to include the known species of the whole of Central America although the genus remains best known in Panama where the most careful collecting has been done. In several respects this study has proven to be the most difficult of any thus far undertaken on Central American genera. Differences between species are often obscure and very puzzling. Color patterns have been shown to be of little value as a means of distinguishing species. The male palps and the epigyna are the most reliable specific structures upon which one can rely in separating species. Doubtless there will be araneologists who will differ with me in respect to the degree of reliability shown by these structures. The difficulties I have mentioned have in the past caused much confusion and many errors in identification. It seems evident from a study of specimens of nearly all of the species recognized by the Cambridges (1889-1905) that even they dealt, to some extent, with mixed material. Among females I have found that close attention must be paid to such details of the epigynum as: shape of base, shape of scape, shape of the clear central area of the base bordered by tubules, relative proportions of base and scape, positions of the apertures to the spermathecae, positions of the spermathecae, etc. F. P. Cambridge (1904) recognized and definitely named several parts of the male palpal tarsus considered important in distinguishing species. I have thought it best to retain the Cambridge terminology for these parts with little modification and few additions. These palpal parts may be named as follows: basal apophysis (basal tarsal hook), uncus, embolus, conductor, clavis, vesicle, terminal laminae, maxillary tooth, femoral tubercle. The named parts of the male palpal tarsus are shown in Figures A and B, based upon *E. fusco-vittata* (Keyserling).

Acknowledgments are due and gratefully extended to the following persons and organizations for their interest and aid: Dr. A. S. Romer, Director, and Dr. P. J. Darlington, Jr., Curator of Insects, respectively, in the Museum of Comparative Zoology at Harvard College where much of the work of preparing this paper was carried on; Dr. W. J. Gertsch, American Museum of Natural History, for the loan of much valuable material from Central America; Dr. G. Owen Evans, Department of Zoology, British Museum (Natural History), for the loan of almost indispensable material studied by the Cambridges; the donors of the Penrose Fund of the American Philosophical Society and The Society of Sigma Xi for their financial aid which made it possible for me to spend the summer of 1950 engaged in field studies and collecting in Panama.

The types of *Eustala abdita* sp. nov., *E. banksi* sp. nov., *E. mexicana* sp. nov., *E. mimica* sp. nov., *E. panamana* sp. nov. will be deposited in the American Museum of Natural History, New



External Anatomy of *Eustala*
Figures A and B

Fig. A. Diagram of male palpal tarsus; lateral view; showing important features.

Fig. B. The same; view from in front.
1—vesicle; 2—embolus; 3—uncus; 4—conductor; 5—clavis; 6—tarsal hook (basal apophysis); 7—terminal laminae.
(Both diagrams based upon *E. fusco-vittata*)

York City. All other types will be deposited in the Museum of Comparative Zoology at Harvard College.

Genus EUSTALA Simon 1895

The Cambridges (1889-1904) reported the following eleven species of *Eustala* from Central America: *E. anastera* (Walckenaer); *E. bifida* F. P. Cambridge; *E. clavispina* (O. P. Cambridge); *E. fragilis* (O. P. Cambridge); *E. fusco-vittata* (Keyserling); *E. guttata* F. P. Cambridge; *E. illicita* (O. P. Cambridge); *E. latebricola* (O. P. Cambridge); *E. scutigera* (O. P. Cambridge); *E. semifoliata* (O. P. Cambridge); *E. vegeta* (Keyserling). *E. conformans* Chamberlin completes the list of twelve species known from Central America prior to the present work on this genus. According to my present view of speciation in this genus we must now add the following twenty-six new species to the known list from this part of the world: *E. abdita* sp. nov.; *E. banksi* sp. nov.; *E. bucolica* sp. nov.; *E. delecta* sp. nov.; *E. exigua* sp. nov.; *E. gertschi* sp. nov.; *E. inconstans* sp. nov.; *E. ingenua* sp. nov.; *E. innoxia* sp. nov.; *E. lata* sp. nov.; *E. longembola* sp. nov.; *E. maxima* sp. nov.; *E. mexicana* sp. nov.; *E. mimica* sp. nov.; *E. minima* sp. nov.; *E. montana* sp. nov.; *E. montivaga* sp. nov.; *E. oblonga* sp. nov.; *E. panamana* sp. nov.; *E. redundans* sp. nov.; *E. rustica* sp. nov.; *E. scitula* sp. nov.; *E. sedula* sp. nov.; *E. tantula* sp. nov.; *E. tumida* sp. nov.; *E. venusta* sp. nov. Thirty-two of the thirty-eight species now known in Central America are found in Panama. Those which thus far appear not to occur in Panama are the following: *E. abdita* sp. nov.; *E. anastera* (Walck.); *E. banksi* sp. nov.; *E. bifida* F. P. Cambridge; *E. clavispina* (O. P. Cambridge); and *E. mexicana* sp. nov. The total number listed here will probably be somewhat reduced when it becomes possible to match up males and females more successfully than I have been able to do. There are few reliable guides in this genus, particularly among those with the round-triangular form, which can be used to match males and females. Among the species from Central America, I have found the color pattern so highly variable within the species and between males and females that I am compelled to avoid its use in any important way. My experience

is, therefore, very different from that of Mello-Leitao (1947). Where there is reasonable doubt I have chosen to describe the males and females as separate species rather than run the danger of missmating, with the resulting complications in later literature.

Key to the Species of Eustala *in Central America*

Males

1. Abdomen elongate, slender (*fusco-vittata, illicita, oblonga*) 2
1. Abdomen not elongate; rounded-triangular 4
2. Clavis with a distinct robust lateral process at base; conductor simple, without distinct processes (Fig. 3) .....*E. fusco-vittata*, p. 398
2. Clavis without distinct lateral process; conductor with two or three distinct processes 3
3. Clavis deeply excavated at base; conductor with three slender processes (seen in lateral view, Fig. 15) .....*E. oblonga*, p. 404
3. Clavis without basal excavation; conductor with two robust processes (seen in lateral view, Fig. 8) .....*E. illicita*, p. 401
4. Uncus with a broad basal enlargement more or less concealing the tip (*bifida, mimica*, Figs. 37 and 92) 5
4. Uncus with only a shoulder at base or without any basal enlargement 6
5. Conductor robust; uncus without a distinct shank .....*E. bifida*, p. 421
5. Conductor smaller; uncus with a distinct shank proximal to basal enlargement .....*E. mimica*, p. 467
6. Uncus long slender, with no basal shoulder or enlargement (*exigua, gertschi, tantula*) 7
6. Uncus robust, with or without a basal shoulder 9
7. Uncus somewhat concealed; vesicle extremely large, spirally twisted .....*E. tantula*, p. 505
7. Uncus not concealed; vesicle of more normal relative size, not spirally twisted 8
8. Conductor with two slender extensions, seen in lateral view (Fig. 57).. .....*E. exigua*, p. 435
8. Conductor without slender projections (Fig. 61) ...*E. gertschi*, p. 440
9. Conductor with a definite lobe (*delecta, scutigera*) 10
9. Conductor without any definite lobe 11
10. Conductor with a conspicuous lobe somewhat overlapping the uncus; embolus relatively long and slender .....*E. scutigera*, p. 496
10. Conductor with an inconspicuous lobe not overlapping the uncus; embolus relatively broad and flat .....*E. delecta*, p. 431

11. With an extremely long slender embolus (Fig. 83) *E. longembola*, p. 458
11. Without an extremely long slender embolus 12
12. Uncus distinctly sickle-shape, with a marked shoulder at its base ..... *E. montana*, p. 474
12. Uncus not distinctly sickle-shape, with no shoulder at its base or with a moderately developed shoulder 13
13. Uncus short, small and somewhat concealed; vesicle concealed ..... *E. abdita*, p. 410
13. Uncus a more or less robust hook; vesicle usually exposed (concealed in *inconstans*) 14
14. Massive conductor continued posteriorly as a slender, setose extension ..... *E. anastera*, p. 414
14. Conductor of moderate size and not continued posteriorly as a slender, setose extension 15
15. Embolus relatively long and slender; vesicle relatively large and bulbous (*guttata, scitula*) 16
15. Embolus not so long and not so slender; vesicle of moderate size or concealed 17
16. Uncus of moderate size, with a definite shoulder at its base ..... *E. guttata*, p. 442
16. Uncus more robust, without a definite shoulder at its base ..... *E. scitula*, p. 492
17. Embolus very short, very broad at base; vesicle withdrawn or greatly reduced in size ..... *E. inconstans*, p. 446
17. Embolus moderately long and slender; vesicle of moderate size and clearly exposed 18
18. Fourth femur with ventral spines confined to distal third of segment (*bucolica, rustica*) 19
18. Fourth femur with ventral spines extending throughout much more than distal third of segment (*banksi, vegeta*) 20
19. Embolus with free part relatively short and slender ..... *E. bucolica*, p. 425
19. Embolus terminally broad and grooved ..... *E. rustica*, p. 486
20. Uncus with a long robust base or shank; conductor deeply grooved on distal surface ..... *E. banksi*, p. 417
20. Uncus without a long robust basal shank; conductor without a deep groove on distal surface ..... *E. vegeta*, p. 511

Females

(*E. fragilis* (O. P. Cambridge) is not included in the key because of the lack of clear and definite knowledge about the species.)

1. Abdomen elongate, slender (*fusco-vittata, illicita, oblonga*) 2
1. Abdomen not elongate; rounded-triangular 4

2. Scape of epigynum not clearly separated from base; gradually narrowed from base to tip ..... *E. fusco-vittata*, p. 398
2. Scape of epigynum clearly separated from base; not gradually narrowed from base to tip 3
3. Scape arises from near middle of base and extends as a slender median structure ..... *E. oblonga*, p. 404
3. Scape arising from near anterior margin of base and widened in middle ..... *E. illicita*, p. 401
4. Pars cephalica extended into a distinct eye-bearing cone (Fig. 131) ..... *E. tumida*, p. 508
4. Pars cephalica normal, not extended into an eye-bearing cone 5
5. Base of epigynum expanded into a pair of shoulders surrounding the apertures; scape relatively very slender (*guttata, redundans*) 6
5. Base of epigynum not expanded into a pair of shoulders surrounding the apertures 7
6. Base of epigynum with a posterior projection from the central area ..... *E. redundans*, p. 484
6. Base of epigynum without any posterior projection from the central area ..... *E. guttata*, p. 442
7. Scape of epigynum sharply narrowed where it joins the base, viewed from below (*ingenua, latebricola, mexicana, minima, vegeta, venusta*) 8
7. Scape of epigynum gradually narrowed from base to tip, viewed from below (*anastera, maxima, innoxia, montivaga, panamana, rustica, scutigera, sedula, semifoliata*) 13
8. Scape of epigynum short, expanded at tip, originates from base behind the anterior margin ..... *E. minima*, p. 471
8. Scape longer, not expanded at tip or, if expanded at tip, originates at anterior border of base 9
9. Apertures nearly in contact in middle; scape of epigynum only slightly rugulose ..... *E. ingenua*, p. 449
9. Apertures of epigynum much farther apart; scape at least moderately rugulose 10
10. Scape of epigynum with a semicircular ridge just anterior to apertures; the latter barely two diameters of one of them apart ..... *E. latebricola*, p. 457
10. Scape of epigynum without a semicircular ridge in front of the apertures; the latter more than two diameters of one of them apart ... 11
11. Central area of base of epigynum drawn out laterally into narrow extensions; base in general quite oval in outline .. *E. mexicana*, p. 465
11. Central area of base of epigynum not drawn out laterally into narrow extensions; base in general not oval in outline 12
12. Apertures of epigynum fully five times the diameter of one of them

apart; spermathecae several diameters of one of them apart .....
.....*E. vegeta*, p. 511

12. Apertures of epigynum not so far apart; spermathecae in contact in middle of central area .....*E. venusta*, p. 515
13. Venter with a pair of white spots transversely placed .....
.....*E. semifoliata*, p. 502
13. Venter without a definite pair of white spots transversely placed 14
14. Abdominal hairs abruptly dilate basally .....*E. clavispina*, p. 428
14. Abdominal hairs not dilate basally 15
15. Apertures of epigynum hidden; epigynum in general simple, with few external features .....*E. innoxia*, p. 452
15. Apertures of epigynum clearly exposed but sometimes small; epigynum more complicated, with several external features 16
16. Central part of base of epigynum relatively small; only about one fourth as broad as base; base nearly as broad as long; chitinized areas lateral to base .....*E. conformans*, p. 430
16. Central part of base of epigynum relatively larger and considerably broader; without conspicuous chitinized areas lateral to base 17
17. Scape of epigynum nearly or quite as long as base is broad 18
17. Scape of epigynum not nearly as long as base is broad 19
18. Apertures of epigynum nearly in contact; central area of base triangular in outline .....*E. sedula*, p. 500
18. Apertures of epigynum well separated; central area of base more oval in outline .....*E. lata*, p. 454
19. Apertures of epigynum nearly or quite at lateral margins of base (*bifida, maxima*) 20
19. Apertures of epigynum far removed from margins of base 21
20. The inner of the paired tubules bounding the central area of base shorter and broader; central area of base raised into two marked prominences .....*E. bifida*, p. 421
20. The inner of the two tubules bounding the central area of base narrower and much longer; the central area of base not raised into prominences .....*E. maxima*, p. 461
21. Central area of base of epigynum bounded by only one definite pair of curved tubules; scape much narrower at its base than width of the latter .....*E. rustica*, p. 486
21. Central area of base of epigynum bounded by two pairs of more or less distinct tubules; scape nearly as wide at its base as the width of the whole base 22
22. The central area of the base of the epigynum considerably longer than broad .....*E. anastera*, p. 414
22. The central area of the base of the epigynum as wide as long or wider than long 23

23. Scape of the epigynum not much narrowed until a considerable distance in front of the apertures ..... *E. scutigera*, p. 496
23. Scape of the epigynum gradually narrowed from opposite the apertures (*montivaga, panamana*) 24
24. Central area of base of the epigynum definitely wider than long .... *E. panamana*, p. 480
24. Central area of base of the epigynum about as wide as long .... *E. montivaga*, p. 478

Eustala fusco-vittata (Keyserling), 1863

(Figures 1-5)

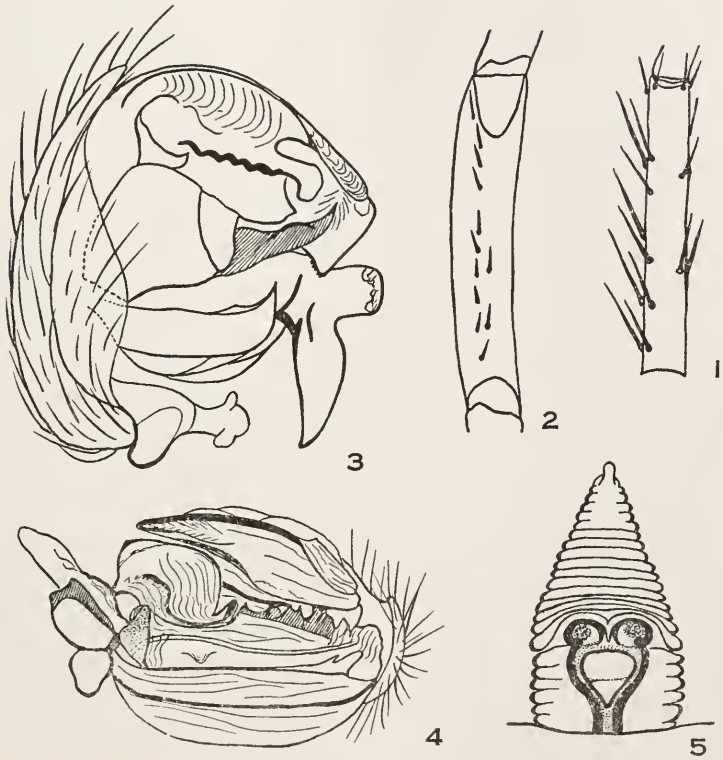
Epeira fusco-vittata Keyserling, 1863
E. fusco-vittata Keyserling, 1892
Cyclosa thorelli McCook, 1893
Eustala fusco-vittata Simon, 1897
E. caudata Banks, 1898
E. fusco-vittata F. P. Cambridge, 1904
E. fusco-vittata Petrunkevitch, 1911
E. fusco-vittata Petrunkevitch, 1925
E. *fusco-vittata* Banks, 1929
E. fusco-vittata Petrunkevitch, 1930
E. fusco-vittata Bryant, 1940

This is the best-known species in the genus, in Central America. It has been collected over a wide area throughout Central America, several of the West Indies, and much of South America. In this species, as in others previously known, figures and the most important facts concerning basic structural features are given herewith as an aid to identification and study of the group.

Male hypotype. Total length 8.58 mm. Central ocular quadrangle wider in front than behind in ratio of 4 : 3; almost exactly as wide in front as long. Ratio of eyes AME : ALE : PME : PLE = 13 : 9 : 11 : 8.5. AME separated from one another by about four-thirds of their diameter, from ALE by nearly five-halves of their diameter. PME separated from one another by a little more than two-thirds of their diameter, from PLE by nearly four times their diameter. Laterals separated from one another by the radius of ALE. Promargin of fang groove with four teeth, the second and fourth smaller, the others robust; retromargin with three teeth. Secondary sexual char-

acters on maxillae and adjacent segments appear as usual and are well developed. Sternum longer than wide in ratio of 23 : 13.

Legs. 1423. Width of first patella at "knee" .433 mm., tibial index of first leg 9. Width of fourth patella at "knee" .390 mm., tibial index of fourth leg 9.



External Anatomy of *Eustala*
Figures 1-5, *E. fusco-vittata*

Fig. 1. Left second tibia; ventral view.
Fig. 2. Right second femur; ventral view.
Fig. 3. Left male palpal tarsus; lateral view.
Fig. 4. Left male palpal tarsus; from in front.
Fig. 5. Epigynum; from below.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.030	1.560	3.510	3.900	1.267	14.267
2.	3.250	1.235	1.950	2.860	1.235	10.530
3.	2.405	.845	1.430	1.625	.845	7.150
4.	4.030	1.430	2.990	3.250	1.170	12.870
Palp.	.715	.352	.220	——	1.235	2.522

Second tibia with ventral and related spines as shown in Figure 1. The ventral femoral spines on the second leg are particularly prominent; in the hypotype there are twelve on the right (Fig. 2) and seven on the left. The fourth femur appears regularly to be devoid of ventral spines.

Palp. Complicated and characteristic; features of femur, patella and tibia are about as usual in the genus. Tarsus: the basal tarsal apophysis has a distorted arrow-shape; the clavis is deeply excavated at its base and has a robust anterolateral process, and is also seen to be geniculate when viewed laterally; the uncus is long, rather slender, and has a central medial curved ridge; the conductor is relatively simple and when viewed ventrolaterally it appears more or less quadrilateral but is deeply grooved distally; the vesicle is small, strongly chitinized; the embolus is thin, grooved, and gently curved at its distal end; the terminal laminae include a series of strongly chitinized dentations (Figs. 3-4).

Color in alcohol. The carapace has a rather narrow central brownish stripe and is yellowish elsewhere. The sternum is yellowish flecked with grayish. Abdomen: there is a fairly well marked dorsal folium divided into three stripes of which the laterals are lighter and contain reddish dots; the venter has a broad central brownish stripe on each side of which there is a yellowish granular stripe. Much variation in color pattern has been noted among the many individuals studied.

Female hypotype. Total length 8.255 mm.

Legs. 1423. Width of first patella at "knee" .433 mm., tibial index of first leg 9. Width of fourth patella at "knee" .401 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.380	1.625	3.055	3.445	1.170	12.675
2.	2.795	1.495	2.925	3.120	1.105	11.440
3.	2.015	.780	1.235	1.430	.780	6.240
4.	3.500	1.365	2.730	3.120	.975	11.690

Epigynum. The apertures are nearly in contact in the middle; the posterior surface has a characteristic central convexity; the scape, broad at the base, gradually tapers to the tip (Fig. 5).

Type locality. Male hypotype from Barro Colorado Island, C. Z., August, 1950; female hypotype from the same locality, July, 1939. Several hundred specimens of both sexes have been examined from many localities in Mexico, Guatemala, Honduras, Costa Rica, Nicaragua, and Panama.

Eustala illicita (O. P. Cambridge), 1889

(Figures 6-11)

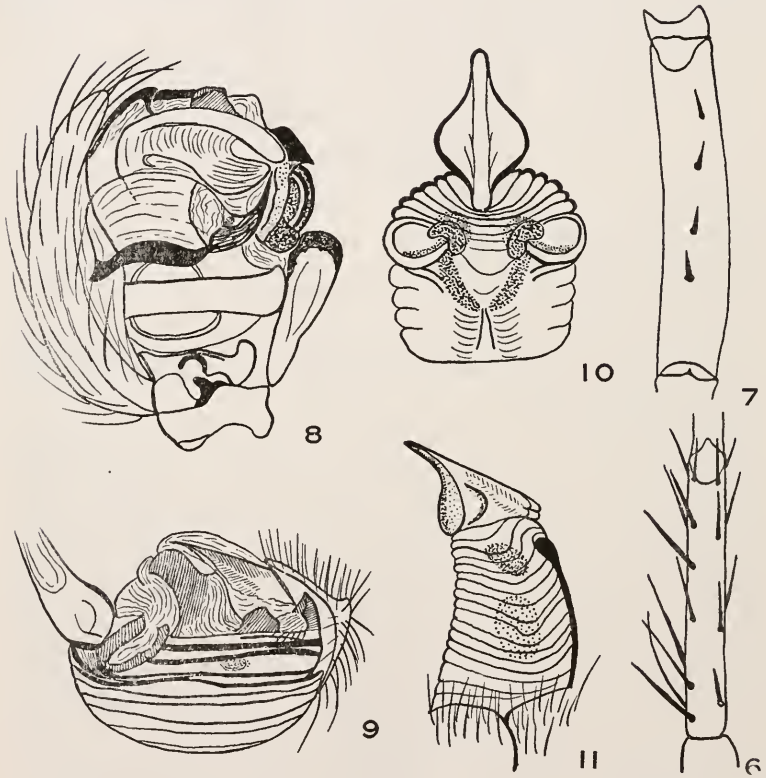
Epeira illicita O. P. Cambridge, 1889
E. cambridgei Keyserling, 1893
Eustala illicita F. P. Cambridge, 1904
E. illicita Petrunkevitch, 1911

I have had only females from the British Museum for comparison but there can hardly be any doubt of the correct identification of the males, however.

Male hypotype. Total length 6.50 mm. With an elongated form like that of *E. fusco-vittata* but more slender than in that species. Central ocular quadrangle wider in front than behind in ratio of 6 : 5; slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 11 : 8 : 10.5 : 7.5. AME separated from one another by nearly five-thirds of their diameter, from ALE by nearly five-halves of their diameter. PME separated from one another by nearly their diameter, from PLE by about seven-halves of their diameter. Laterals separated from one another by the radius of ALE. Three long slender spines form a triangular area between AME. Height of clypeus equal to nearly three-halves of the diameter of AME. Promargin of fang groove with five teeth, the fourth the largest; retromargin with two on the right side and three on the left. The secondary sexual characters appear about as usual on the first coxa and second femur.

Legs. 1423. Width of first patella at "knee" .379 mm., tibial index of first leg 8. Width of fourth patella at "knee" .357 mm., tibial index of fourth leg 9.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.835	1.365	3.315	3.347	.975	12.837
2.	3.185	1.170	2.405	2.605	.910	10.275
3.	2.145	.715	1.170	1.237	.715	5.982
4.	3.575	1.235	2.470	3.120	.845	11.245
Palp	.466	.314	.271	——	.980	2.031



External Anatomy of *Eustala*
Figures 6-11, *E. illicita*

Fig. 6. Left second tibia, ventral view.
Fig. 7. Left second femur, ventral view.
Fig. 8. Left male palpal tarsus, lateral view.
Fig. 9. Left male palpal tarsus, from in front.
Fig. 10. Epigynum, from below.
Fig. 11. Epigynum, lateral view.

Second tibia with ventral and related spines as shown in Figure 6. The first femur has a double series of ventral spines as follows: promargin with one or two near distal end and hardly more than bristles; the retromargin has three all in the distal two fifths of the segment. The second femur has a single series of ventral spines with four on the left side and five on the right (Fig. 7); all are fairly robust. The third femur has a series of two or three ventral spines. The fourth femur appears to be regularly devoid of ventral spines.

Palp. Features of the femur, patella, and tibia appear to be typical of the genus. Tarsus: basal tarsal apophysis well developed but unnoteworthy; clavis moderately robust, with its surface somewhat irregular, and with base strongly chitinized but unexcavated; the uncus is a well developed, evenly curved, sickle-shaped hook; the conductor is massive, deeply excavated along its lateral surface and with two processes as seen in lateral view; distally the conductor and terminal laminae combine to make two conspicuous grooves; the vesicle is small but clearly evident; the embolus is relatively short, flattened, and curved (Figs. 8-9).

Color in alcohol. Carapace and legs almost unicolorous amber-yellow. Sternum yellowish, flecked with brownish gray. Abdomen: dorsal folium very poorly defined; in a male from Mexico the abdominal markings are very similar to those recorded for *E. fusco-vittata;* the venter has a broad dark stripe from genital groove to base of spinnerets together with a narrow whitish granular margin.

Female hypotype. Total length 12.22 mm.; with the elongated form characteristic of *E. fusco-vittata* (Keys.) and *E. oblonga* sp. nov.

Legs. Width of first patella at "knee" .542 mm., tibial index of first leg 9. Width of fourth patella at "knee" .520 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.875	1.950	4.225	4.160	1.170	16.380
2.	4.290	1.820	3.640	3.900	1.170	14.820
3.	2.600	1.105	1.495	1.885	.910	7.995
4.	4.875	1.820	3.445	4.030	1.170	15.340

Ventral femoral spines are rare in the females and, apparently, quite irregular.

Epigynum. The base appears to have a more or less distinctive pattern of tubules, apertures, and striations. The scape is very distinctive; it begins narrow, almost immediately broadens, and then narrows again to terminate in a blunt point (Figs. 10-11).

Color in alcohol. There is a narrow dark middorsal stripe on the abdomen with the dorsal folium also poorly defined. The venter has a moderately broad dark median stripe and a yellowish area on each side.

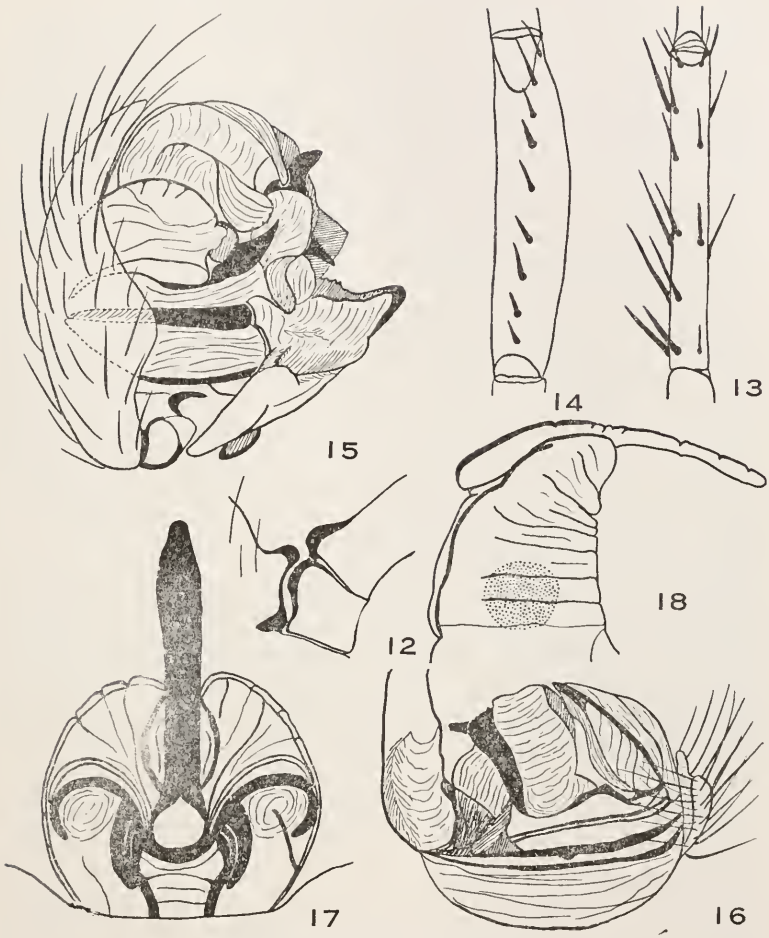
Type locality. The Cambridges had this species from Mexico and Guatemala. The hypotype male is from Madden Dam Forest, C. Z., July, 1950; the female hypotype is from San Luis Potosi, Mexico, July, 1941 (L. I. Davis). Specimens from Mexico, Guatemala, Costa Rica, El Valle, R. P., November, 1946; Canal Zone, July, 1950 (but not yet from Barro Colorado Island) have been studied.

Eustala oblonga sp. nov.

(Figures 12-18)

Male holotype. Total length 6.825 mm. Carapace 3.25 mm. long, 2.47 mm. wide opposite interval between second and third coxae where it is widest; .975 mm. tall and, therefore, nearly .4 as tall as wide; gently raised from PME to opposite third coxae from where descent arches sharply to posterior border; well rounded from opposite posterior border of fourth coxae to opposite anterior border of second coxae from where it is narrowed to a blunt point between AME; longitudinal thoracic groove long and well marked; with a moderately well developed covering of light yellowish hair; with several slender spines in ocular area.

Eyes. Eight in two rows, all dark; ocular tubercle bearing ALE quite prominent; viewed from above, both rows strongly recurved; viewed from in front, anterior row moderately procurved; central ocular quadrangle wider in front than behind in ratio of 20 : 17, slightly wider in front than long; ALE extend somewhat beyond margins of carapace at their level. Ratio of eyes AME : ALE : PME : PLE = 14 : 9 : 11 : 10. AME sep-



External Anatomy of *Eustala*
Figures 12-18, *E. oblonga* sp. nov.

Fig. 12. Male maxilla, palpal femur and trochanter
Fig. 13. Left second tibia from below.
Fig. 14. Left second femur from below.
Fig. 15. Left palpal tarsus, lateral view.
Fig. 16. Left palpal tarsus from in front.
Fig. 17. Epigynum from below.
Fig. 18. Epigynum, lateral view.

arated from one another by nine-sevenths of their diameter, from ALE by about 1.6 times their diameter. PME separated from one another by their diameter, from PLE by about three times their diameter. Laterals separated by three-tenths of the diameter of PLE. Height of clypeus equal to about six-sevenths of the diameter of AME. Clypeus strongly receding and with a recess between it and base of chelicerae; apparently with a single long slender spine between each AME and other smaller and weaker spinules and bristles.

Chelicerae. Somewhat receding but essentially vertical and parallel; with basal boss moderately well developed; basal segment .758 mm. long; each with several very slender spines or bristles in front; with well marked fang groove studded with minute denticles; retromargin of fang groove with three teeth of moderate size, all in basal half with middle one somewhat the smallest; promargin with four teeth, the third from base being the largest; fang of moderate length, evenly curved and finely dentate along inner margin.

Maxillae. Essentially parallel; about two-thirds as broad as long; with a robust, strongly chitinized lateral tubercle opposed to a corresponding tubercle at base of palpal femur; with marginal serrula well developed at lateral distal corner; with well developed scopula along distal lateral medial corner and adjacent distal border (Fig. 12, from a dissected paratype).

Lip. Broader than long in ratio of about 4 : 3; with cross striations in basal third. Sternal suture indefinite, gently procurved.

Sternum. Narrowly scutiform; mildly convex; moderately scalloped opposite coxae; longer than wide in ratio of about 3 : 2; slightly the widest at interval between second and third coxae; posterior end continued as a very slender sclerite between fourth coxae which are separated only by a little more than one fifth of their width.

Legs. 1423. Width of first patella at "knee" .433 mm., tibial index of first leg 9. Width of fourth patella at "knee" .379 mm., tibial index of fourth leg 9.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.095	1.430	3.640	3.900	1.365	14.430
2.	3.380	1.235	2.795	3.250	1.150	11.810
3.	2.285	.845	1.267	1.495	.845	6.737
4.	3.965	1.267	2.795	2.990	1.040	12.057
Palp	.585	.330	.220	——	1.105	2.240

Spines. First leg: femur dorsal and prolateral 0-0-1-1-1, retrolateral 0-0-0-0-1-1, ventral with six or seven along retromargin and two or three along promargin, all in distal half; patella dorsal 0-1, prolateral and retrolateral 1-1; tibia dorsal 0-1-0-1-1-0, prolateral 1-1-1-1-1-0 on right but with six on left, retrolateral 0-1-0-1-0, ventral 2-2-lr-lp-2-lp-2; metatarsus dorsal 0-1-0-1-0-0, prolateral 0-0-1-0-1-0, retrolateral 0-1-0-1-0, ventral 2-2-2 with considerable irregularity. Second leg: femur dorsal as in first, prolateral only one near distal end, retrolateral 0-0-0-1-1-1, ventral a row of nine short but robust spines extending to retromargin distally (Fig. 14); patella as in first; tibia dorsal 1-0-1-1-0, prolateral 1-1-1-1-1, retrolateral 0-1-1-1, ventral 2-lp-2-2-lp-2 (prolateral and ventral spines appear to be modified for a common use, Fig. 13); metatarsus dorsal 0-1-0, prolateral 0-1-0-0-0, retrolateral 0-1-0-1-0, ventral 0-2-2-0. Third leg: femur dorsal 0-1-0-1-1, prolateral and retrolateral only one near distal end, ventral 0-0-2 (missing on left leg)-2; patella dorsal 1-1, prolateral and retrolateral only one near distal end; tibia dorsal 1-0-1, prolateral 1-1-1, retrolateral 0-1-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral 0-1-1-1 (all median). Fourth leg: femur dorsal 0-1-0-1-1, prolateral 0-0-1-1-1(left) and 0-0-0-1-1(right), retrolateral 0-0-1-1-1, ventral only two near distal end; patella as in third; tibia dorsal 0-1-0-1-1-0, prolateral 1-1-0-1-1(left) and 1-1-1-1-1(right), retrolateral 1-0-1-0, ventral 2-2-2-2(right) and 2-lp-lr-lp-2(left); metatarsus dorsal 0-1-0-1-0-0, prolateral 0-1-0-1, retrolateral 0-1-0-1-1-0, ventral 2-lp-lp-2. Palpal patella with a weak proximal dorsal spine and a single distal dorsal long slender spine. Palpal tibia with many long bristles and a single distal dorsal long slender spine. There are apparently six trichobothria of varying length also on the dorsal side of the tibia.

Palp. Very complicated; the trochanter has a strongly chitin-

ized tubercle which appears to act with those on the maxilla and femur as already recorded (Fig. 12); patella very short, simple, strongly chitinized; tibia very short and trilobed, with the ventral lobe provided with a strongly chitinized ventral rim. Tarsus very characteristic; basal apophysis a distorted arrow-shape; the clavis is robust, very broad and deeply excavated at its anterior end; the uncus is a sharply pointed tooth; the conductor has a broad central portion with three very characteristic extensions; the vesicle is small, strongly chitinized, and provided with a lobule; the embolus is flat, rather short and curved; the terminal laminae are raised into three prominences (Figs. 15-16).

Abdomen. Elongate as in *E. fusco-vittata* (Keys.); longer than wide in a ratio of a little more than 2 : 1; widest about one-third of length from base; overlaps abdomen only slightly; extends behind posterior margin of spinnerets about one-ninth of its length; anal tubercle a short robust prominence strongly chitinized at base; six spinnerets as usual in the genus; colulus a small tubercle with several short erect dark bristles; tracheal spiracle slightly in front of colulus and with a moderately chitinized ventral lip; with a small rounded brown sclerite between colulus and tracheal spiracle.

Color in alcohol. Carapace yellowish with darker flecks and with considerable reddish brown around the eyes; sternum grayish; legs and mouth parts generally yellowish but first and second pairs of legs and fourth tibiae have broad brown bands indefinitely delimited. Abdomen: there is a broad dark dorsal folium extending throughout and divisible into three narrower components; lateral to the folium is a light stripe on each side beneath which occurs a dark stripe; the venter has a median broad dark stripe with a narrow light yellowish stripe on each side. In some paratypes the dorsolateral light stripes have reddish areas but the color appears to be less variable in this species than in many others within the genus.

Female allotype. Total length 9.88 mm. Carapace 3.445 mm. long; 2.60 mm. wide opposite second coxae where it is widest; .975 mm. tall and, therefore, about .38 as tall as wide; broader in front than in male. Otherwise essentially as in male.

Eyes. Seen from above, both rows less strongly recurved than in male; ocular tubercles less prominent than in male; central ocular quadrangle almost exactly as long as wide in front. Ratio

of eyes AME : ALE : PME : PLE = 6 : 5 : 6 : 5. AME separated from one another by nearly 1.5 times their diameter, from ALE by slightly less than 3.5 times their diameter. PME separated from one another by nearly their diameter, from PLE by slightly more than four times their diameter. Laterals separated by about two-fifths of their diameter. Height of clypeus slightly less than diameter of AME. Clypeus with numerous long stiff bristles.

Chelicerae. Basal segment 1.105 mm. long; teeth along fang groove more robust than in male. Otherwise essentially as in male.

Maxillae and *Lip.* Essentially as in male except for maxillary tooth in the latter.

Sternum. Longer than wide in ratio of 24 : 17; with rather marked convexities opposite third coxae, less prominent convexities opposite first coxae and hardly any opposite second coxae. Otherwise essentially as in male.

Legs. 1243. Width of first patella at "knee" .466 mm., tibial index of first leg 8. Width of fourth patella at "knee" .466 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.420	1.852	4.030	3.900	1.250	15.472
2.	4.030	1.690	3.575	3.705	1.170	14.170
3.	2.470	.910	1.495	1.690	.910	7.475
4.	4.225	1.560	3.185	3.575	1.170	13.717

Spines. First leg: femur dorsal 0-1-1(both small), prolateral 0-0-1-1-1, retrolateral only one near distal end; patella dorsal 1-1, prolateral 0-1-1-0, retrolateral 0-1 on right and 1-1 on left; tibia dorsal 0-1-0-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-lp-lp-lr-2; metatarsus dorsal 0-1-0-0-0, prolateral 0-1-0-1-0, retrolateral 0-0-0-1-0, ventral 2-2-0-0 with some troublesome irregularities. Second leg: essentially as in first with some variations. Third leg: femur dorsal, prolateral, and retrolateral with a single spine near distal end; patella appears to have only dorsal 1-1; tibia dorsal 0-1-0-0, ventral lp-lp-2 (hardly more than stiff bristles); metatarsus dorsal 0-1-0, prolateral 0-1-1-0, ventral 2-lp-lp-lp-lp(and many spine-like bristles). Fourth leg: femur as in third; patella dorsal 1-1(both weak), prolateral and retro-

lateral 0-1-0; tibia dorsal 0-1-0-0-1-0, prolateral 0-1-1-1, retrolateral 0-1-1; metatarsus dorsal 0-1, prolateral 0-0-1-0-1-1, retrolateral 0-1-1-0, ventral 2(irregular)-lp-lp-lr. Palpal claw pectinate in a single row of slender teeth diminishing in length toward base. Palpal spines: femur with a single dorsal distal spine; patella dorsal 1-1; tibia dorsal 0-0-1-0, prolateral 1-1, retrolateral only one distal; tarsus with numerous spines and spine-like bristles irregularly arranged.

Abdomen. Bluntly pointed at both ends; a little more than twice as long as wide. Otherwise essentially as in male.

Epigynum. Very distinctive; base nearly circular in outline as seen in ventral view; scape long, slender, arising from near the center of base (Figs. 17-18).

Color in alcohol. Closely resembles that of male but the dorsal folium is more broken and less distinct than in that sex.

Type locality. Male holotype from Barro Colorado Island, C. Z., July, 1950. Female allotype from the same locality, July, 1936. Paratypes of both sexes from the following localities: Barro Colorado Island, July, 1924 (Banks); June-July, 1936; July-August, 1939; August, 1946 (L. H. Krauss); July, 1950; Canal Zone Forest Reserve, C. Z., July, 1939 and August, 1950; France Field, C. Z., August, 1939.

Eustala abdita sp. nov.

(Figures 19-23)

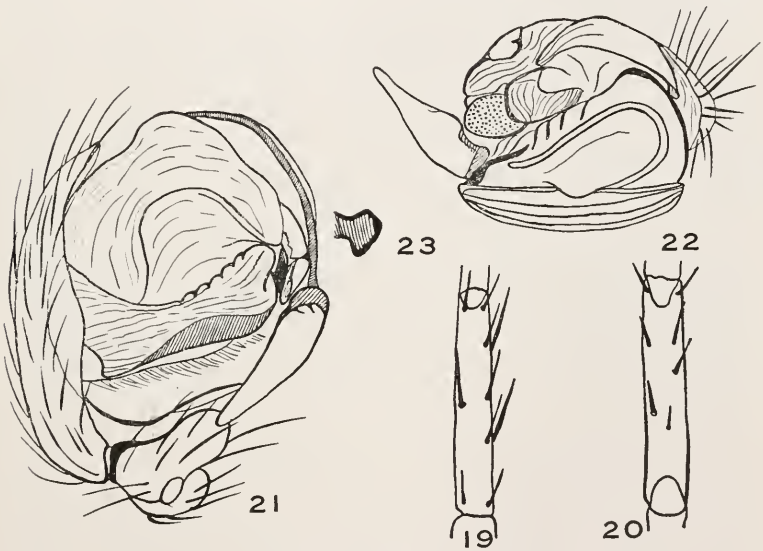
Male holotype. Total length 3.445 mm. Carapace 1.69 mm. long; 1.43 mm. wide between second coxae where it is widest; .704 mm. tall and, therefore, nearly .50 as tall as wide; with well developed longitudinal thoracic groove; spines confined to ocular region.

Eyes. Eight in two rows, all dark. Viewed from above, both rows strongly recurved; viewed from in front, anterior row moderately procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 16 : 13, wider in front than long in ratio of 16 : 13. Ratio of eyes AME : ALE : PME : PLE = 9 : 6 : 8 : 5.5. AME separated from one another by one and one-third times their diameter, from ALE by one and one-half times their diameter. PME separated from one

another by one and one-fourth times their diameter, from PLE by slightly more than three times their diameter. LE separated from one another by two-thirds the diameter of ALE. Height of clypeus equal to one and one-third times the diameter of AME. A pair of long slender spines occurs dorsal to LE; also a row of spine-like bristles between ME.

Chelicerae. Basal segment .433 mm. long. Fang groove well marked. Promargin of fang groove with three teeth, the middle one small; retromargin with four teeth, the second and fourth small, the other more robust (teeth observed on dissected paratype to avoid injury to holotype). Fang evenly curved, finely dentated along inner margin.

Maxillae. Parallel; full and convex on retrolateral surface; scopula well developed along medial surface and inner distal



External Anatomy of *Eustala*
Figures 19-23, *E. abdita* sp. nov.

Fig. 19. Right second tibia from below.
Fig. 20. Left fourth femur from below.
Fig. 21. Left palpal tarsus, lateral view.
Fig. 22. Left palpal tarsus from in front.
Fig. 23. Basal tarsal apophysis.

angle. Serrula moderately well developed along outer distal angle. With well developed basal tubercle to oppose the chitinous ridge on palpal femur; also with a chitinous ridge extending basally from the tubercle.

Lip. Wider than long in ratio of about 22 : 15; distal third along border full and well rounded; reaches only slightly beyond middle of maxillae. Sternal suture gently procurved.

Sternum. Generally scutiform; longer than wide in ratio of 35 : 26; a sclerite continues from posterior end between fourth coxae which are barely separated; covered by numerous long curved bristles.

Legs. 1243. Width of first patella at "knee" .238 mm., tibial index of first leg 8. Width of fourth patella at "knee" .206 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.892	.812	2.275	1.787	.785	8.551
2.	2.047	.715	1.430	1.462	.715	6.369
3.	1.200	.455	.650	.617	.520	3.442
4.	1.950	.650	1.200	1.200	.585	5.585
Palp	.314	.184	.141	——	.790	1.429

First coxa with well developed ventral distal hook on retromargin; prolateral groove and ridge at base of second femur extends a little less than one-fifth of the length of the segment; the dorsal tubercle on first coxa moderately well developed.

Spines. First leg: femur dorsal 0-0-1-0-1-1, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1-1, ventral 0-0-lp-lp-2; patella dorsal, three bristles in a median row-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-0-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-2-2-lp-2; metatarsus dorsal 0-1-1-0-0, prolateral 0, retrolateral 0-0-1-0, ventral lr-2-lp-0. Second leg: femur dorsal and retrolateral as in first, prolateral 0-0-0-1-1, ventral 0-0-lp-lp-lp; patella essentially as in first; tibia ventral 2-lp-2-lp-2 (Fig. 19), elsewhere as in first; metatarsus dorsal 0-1-0, prolateral 0, retrolateral 0-1-1, ventral 0-lp-lr-lp-0. Third leg: femur dorsal 0-0-1-1-1, prolateral and retrolateral only one near distal end, ventral 0-lp-lp-2-0; patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 0-1-0-1-0, prolateral 0-0-1-0, retrolateral 0-0-1, ventral lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0-1-0, retro-

lateral 0, ventral 0-1-1-0(both weak). Fourth leg: femur ventral 0-2-lr-lr-2 on right and 0-2-lr-2-2 on left (Fig. 20), elsewhere as in first; patella essentially as in third; tibia dorsal as in third, prolateral 1-1-1-1, retrolateral 0-1-1, ventral lp-lp-lp-2; metatarsus dorsal 1-1-0, prolateral 0-1-1-1, retrolateral 0-0-1-0, ventral 0-lp-lp.

Palp. Complicated; the basal ventral femoral tubercle or ridge opposing the maxillary tooth is moderately well developed; the patella is short and has a single long dorsal distal spine and a weak proximal one; the tibia is short, trilobed as usual with the articular lobe provided with the usual strongly chitinized thin lamina opposed to the strongly chitinized base of the tarsus. Tarsus: the basal tarsal apophysis is more nearly arrow-shaped than in some species; the clavis is moderately robust, unexcavated at its base but it has a basal modified articular surface; the uncus is a short hook, more or less hidden against the conductor; the conductor itself is simpler than in some species but its distal end has two clearly distinguishable surfaces; the vesicle is largely hidden within; the embolus is either modified into a broad thin plate or hidden; the terminal laminae are expanded into a bulbous structure containing a prominent tubule and a median tubercle; cuspules on conductor and laminae are almost lackin (Figs. 21-23).

Abdomen. Total length 1.95 mm.; rounded at both ends with triangular form obscured; longer than wide in ratio of 15 : 13; widest about one third from base; well covered dorsally by moderately long slender spines. Otherwise essentially as usual in the genus.

Color in alcohol. Carapace yellowish with brownish spots in vicinity of thoracic groove; with a pair of dots near the posterior end of the groove. All eyes except AME ringed with black pigment. Sternum with an irregular grayish border; elsewhere yellowish flecked with gray. Mouth parts yellowish. Legs yellowish with few brownish bars which are most prominent on femora. Abdomen: dorsal folium poorly indicated; dorsum variegated yellowish elsewhere; venter yellowish, granulated with yellowish-white subchitinous deposits. Two of the paratype males are more deeply colored with the pattern somewhat different from that o the holotype.

Type locality. Male holotype from Huajuapan, Oaxaca, Mexico, Sept., 1946 (H. Wagner). Five male paratypes from the following localities in Mexico: Huajuapan, Oaxaca, Sept., 1946 (H. Wagner); Vera Cruz (Crawford); Teomixla, Morelos, August, 1942 (H. Wagner); Santiago, Colima, January, 1943 (F. Bonet).

Note: Until recently this species has been regarded as the male of *E. mexicana* sp. nov. At the present time this seems less likely.

Eustala anastera (Walck.), 1837

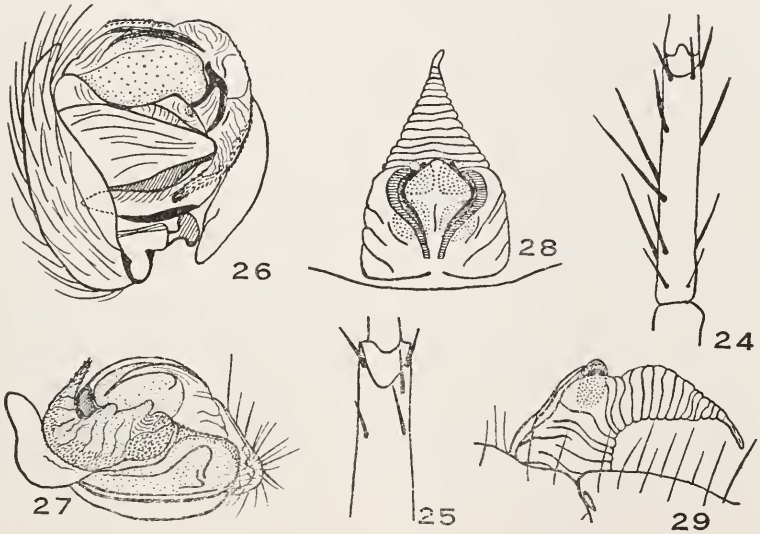
(Figures 24-29)

Epeira anastera Walckenaer, 1837
E. cepina Walckenaer, 1837
E. bombicinaria Hentz, 1847
E. prompta Hentz, 1847
E. parvula Keyserling, 1863
E. parvula Emerton, 1885
E. bombicinaria Keyserling, 1892
E. anastera McCook, 1893
E. anastera Simon, 1894
E. parvula Emerton, 1902
Eustala anastera F. P. Cambridge, 1904
Epeira anastera Banks, 1909
Eustala anastera Petrunkevitch, 1911
E. leuca Chamberlin, 1924
E. buliafera Chamberlin, 1924
E. anastera Petrunkevitch, 1930

Male hypotype. Total length 4.03 mm. The hypotype has the more rounded abdomen which seems to be the usual form in the males of this species. Central ocular quadrangle wider in front than behind in ratio of 29 : 25, wider in front than long in about the same ratio. Ratio of eyes AME : ALE : PME : PLE = 9 : 6 : 8 : 6.5. AME separated from one another by one and one-third times their diameter, from ALE by nearly two diameters. PME separated from one another by about one and one-fourth times their diameter, from PLE by slightly more than three diameters. Laterals separated from one another by slightly less than the diameter of ALE. Height of clypeus equal to eight-

ninths of the diameter of AME. Promargin of fang groove with four teeth, second and fourth small, others of moderate size; retromargin with three teeth of moderate size. Secondary sexual characters on first coxa, maxillae, and adjacent palpal segments together with the prolateral ridge and groove on the second femur appear as usual in the genus. Sternum longer than wide in ratio of 35 : 31.

Legs. 1243. Width of first patella at "knee" .271 mm., tibial index of first leg 9. Width of fourth patella at "knee" .249 mm., tibial index of fourth leg 13.



External Anatomy of *Eustala*
Figures 24-29, *E. anastera*

Fig. 24. Left second tibia from below.
Fig. 25. Left fourth femur from below.
Fig. 26. Male palpal tarsus, lateral view.
Fig. 27. Male palpal tarsus from in front.
Fig. 28. Epigynum from below.
Fig. 29. Epigynum, lateral view.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.600	.942	2.080	1.657	.715	7.994
2.	2.080	.845	1.430	1.462	.650	6.467
3.	1.365	.575	.682	.660	.487	3.769
4.	1.970	.770	1.170	1.170	.520	5.580
Palp	.303	.217	.141	——	.845	1.506

The second femur has only one weak spine near distal end on the retromargin; ventral spines on fourth femur as shown in Figure 25. The ventral and related spines on the second tibia are as shown in Figure 24.

Palp. Complicated and characteristic; features of the femur, patella and tibia appear to be typical of the genus. Tarsus: the basal tarsal apophysis is quite unlike the typical arrow head shape; the clavis is robust, unexcavated at its base; the uncus is stout and twisted; the conductor is massive, extensively setose, and drawn out distally into a characteristically narrow extension unlike that of any other species in Central America; the vesicle is of moderate size; the embolus is of moderate length and size, and is lance-like apically; the terminal laminae are also massive and setose (Figs. 26-27).

Color in alcohol. The carapace is light brown with darker flecks. The sternum is mottled brown. The legs are light brown with faint darker spots. The abdomen has a poorly defined folium. The venter has a faintly defined dark quadrilateral area between the genital groove and the base of the spinnerets; the dark area contains a poorly defined light spot. Other specimens show much variation in the color pattern with the ventral light spot usually much clearer.

Female hypotype. Total length 7.15 mm. (probably above the average for females in this species).

Legs. 1243. Width of first patella at "knee" .455 mm., tibial index of first leg 11. Width of fourth patella at "knee" .379 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.380	1.495	2.665	2.600	.975	11.115
2.	2.990	1.365	2.340	2.275	.910	9.880
3.	1.950	.845	1.040	1.170	.715	5.720
4.	2.860	1.300	1.950	2.015	.780	8.905

There are two long and fairly robust spines on the first femur near the middle, one prolateral and one ventral. Not all females appear to have these spines.

Epigynum. Easily confused with that of *E. bifida* and, perhaps, others in the genus; this is especially true of some of the deviates in the species concerned. The apertures are about one third of the width of the scape at their level from the lateral margin (Figs. 28-29).

Abdomen. With the usual general form except that there are three dorsoventrally arranged posterior tubercles thus giving a marked trifid appearance to this part of the body. This emphasizes the widespread variation of details of form of the abdomen in this species.

Color in alcohol. The carapace is dark brown along the middle, lighter on the lateral sides. Sternum is grayish. Legs with many dark brown bands. Abdomen: the dorsal folium is fairly well defined; the remainder of the dorsum and lateral sides are dark variegated with many lighter spots; there is a vaguely defined ventral whitish spot in the middle of a median darker area.

Type locality. Male hypotype from Amatitlan, Guatemala, August, 1947 (C. & P. Vaurie); female hypotype from San Juan del Rio, Durango, Mexico, August, 1947 (W. J. Gertsch). Males and females from many localities in Mexico and Guatemala have been examined. The Cambridges reported the species from Costa Rica but, so far as I know, it has not been taken in Panama.

Note: The male paratypes of *E. anastera buliafera* Chamberlin in the Museum of Comparative Zoology are clearly *E. anastera* (Walck.) but there is a question regarding the females. It seems likely that the females belong to more than one species.

Eustala banksi sp. nov.

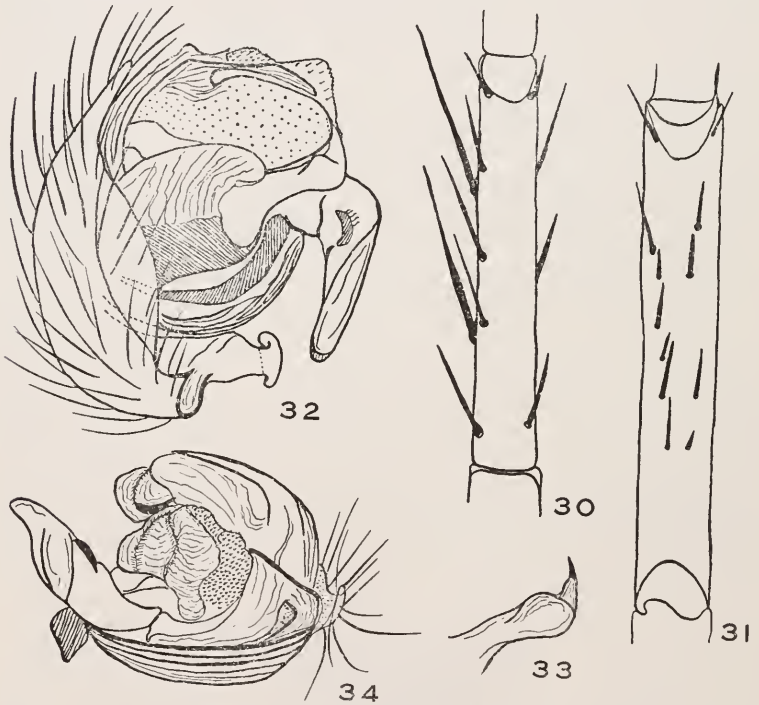
(Figures 30-34)

This species has previously been considered by Mr. Banks and perhaps others as well as myself to belong to *E. bifida* F. P. Cambridge. A closer study reveals so many differences from that species, however, that according to my present views concerning species it must be regarded as new to science. A holotype has, therefore, been selected and is described in accord with my

usual formula. This specimen is not in the best of condition but is the best available.

Male holotype. Total length 5.98 mm. Carapace 3.055 mm. long, 2.535 mm. wide opposite intervals between second and third coxae where it is widest; .975 mm. tall and, therefore, about .38 as tall as wide; only slightly raised from PME to beginning of posterior declivity; with a well developed median longitudinal groove; apparently with few spines, restricted to ocular region.

Eyes. Eight in two rows, all dark; LE on moderately prom-



External Anatomy of *Eustala*
Figures 30-34, *E. banksi* sp. nov.

Fig. 30. Left second tibia from below.
Fig. 31. Right fourth femur from below.
Fig. 32. Left male palpal tarsus, lateral view.
Fig. 33. Uncus, somewhat enlarged from Figure 32.
Fig. 34. Left male palpal tarsus from in front.

inent tubercles; a low conical prominence in middle of median ocular quadrangle from which two long slender spines protrude; viewed from above, both rows strongly recurved; viewed from in front, anterior row moderately procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of about 9 : 7, wider in front than long in ratio of 9 : 8. Ratio of eyes AME : ALE : PME : PLE = 13 : 10 : 11.5 : 7. AME separated from one another by slightly more than 1.5 times their diameter, from ALE by nearly two and one-fourth times their diameter. PME separated from one another by about four-thirds of their diameter, from PLE by four times their diameter. Laterals separated from one another by the diameter of PLE. Height of clypeus equal to about five-thirds of the diameter of AME.

Chelicerae. Essentially parallel, but distal half somewhat excurved; with moderately well developed basal boss; basal segment .65 mm. long. Fang groove well defined; promargin with four teeth, the fourth small; retromargin with three fairly robust teeth.

Maxillae. In general, typical of the genus including the lateral tooth opposing the modifications on the palpal femur and trochanter.

Lip. Wider than long in ratio of about 4 : 3; bluntly pointed distally; extends only a little beyond middle of maxillae; basal half somewhat grooved. Sternal suture very slightly procurved.

Sternum. Elongate-scutiform; longer than wide in ratio of 29 : 20; a sclerite continues from posterior end between fourth coxae which are separated by one-eighth of their width; with numerous long slender bristles.

Legs. 1243. Width of first patella at "knee" .433 mm., tibial index of first leg 8. Width of fourth patella at "knee" .379 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.095	1.560	3.575	3.705	1.235	14.170
2.	3.510	1.235	2.600	2.470	[1]1.000	10.815
3.	2.535	.910	1.300	1.495	.780	7.020
4.	3.175	1.365	2.210	2.632	1.170	10.357
Palp	.444	.282	.217	——	1.105	2.048

[1] Lacking in holotype; length estimated.

First coxa with a well developed ventral distal hook; prolateral proximal groove and ridge on second femur well developed and extending slightly more than one-fifth of total length of segment; the dorsal tubercle on first coxa moderately well developed.

Spines. First leg: femur dorsal 0-0-1-1-1-1, prolateral 0-0-1-1-1, retrolateral 0-0-0-0-1-1, ventral in distal half three on promargin and five on retromargin; patella dorsal 1-1-1, prolateral and retrolateral 0-1-1-0; tibia dorsal 0-1-1-1-1-0, prolateral and retrolateral 0-1-1-0, ventral 0-2-lp-lp-lp-2; metatarsus dorsal 0-1-1-1-0, prolateral 0-0-1-0, retrolateral 0-1-1-0, ventral 2-2-lr-2. Second leg: femur essentially as in first except ventral only one near distal end on promargin; patella as in first except dorsal 1-1 (bristle)-1; tibia essentially as in first except that prolateral and ventral promarginal spines are especially robust (Fig. 30); metatarsus dorsal 0-1-1-0, prolateral 0, retrolateral 0-0-1-0, ventral 2-2-2. Third leg: femur dorsal 0-1-0-1-1, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1, ventral with a double series, four on promargin and six on retromargin; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-1; tibia dorsal 1-0-1, prolateral 1-1-0, retrolateral 0-1-1, ventral 2-2(irregularly placed)-2; metatarsus dorsal 1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral 2-lp-lp-2. Fourth leg: femur dorsal as in third, prolateral only one near distal end, retrolateral 0-0-0-1-1, ventral essentially as in third; patella as in third; tibia dorsal 1-1-1, prolateral 1-1-0-1-1, retrolateral 0-1-0, ventral 2-2-lp-2; metatarsus dorsal 1-1-0, prolateral 0-1-1-0, retrolateral the same, ventral 2-lp-lp-lp.

Palp. Complicated; basal femoral ridge opposing the maxillary tooth moderately well developed; patella short, with a weak basal dorsal spine and a long slender distal dorsal spine; the tibia is as usual, trilobed, with a well developed chitinous collar on the ventral side of the articular lobe. Tarsus: the basal apophysis is a rounded structure without much resemblance to the typical arrow-head; the clavis is a fairly robust structure; the uncus is a robust hook with a long shank and a prominent hump at the base of the terminal hook; the conductor is a massive structure, extensively setose, and distally provided with a deep dorsoventral groove and other distinctive surfaces; the vesicle is moderately large; the embolus is short, slender, and lance-

like terminally; the terminal laminae are massive on the medial side but thin on the lateral half (Figs. 32-34).

Abdomen. Total length 2.787 mm.; with rounded triangular form; with what appears to be a suppressed posterior conical extension; longer than wide in ratio of about 4 : 3; with numerous long slender dorsal and dorsolateral spines; with other features essentially typical of the genus.

Color in alcohol. Carapace yellowish with faint brownish spots and streaks radiating from the median thoracic groove. The most conspicuous of these markings consist of the following: a minute dot on each side just in front of the median groove and a transverse row of four dots a little behind the middle of the furrow; from the second and third of these a narrow stripe extends posteriorly. Sternum light yellowish, flecked with gray. Legs yellowish with both broad and narrow brownish bands and rings. Abdomen: the dorsal folium obscurely outlined in dark brown with many white guanin granules; venter with a lighter area between the genital groove and base of spinnerets surrounded by a narrow brownish border.

Type locality. Male holotype from Ocosingo, Chiapas, Mexico, June, 1950 (Goodnight and Stannard). One male paratype from Turrialba, Costa Rica (Tristan).

Eustala bifida F. P. Cambridge, 1904

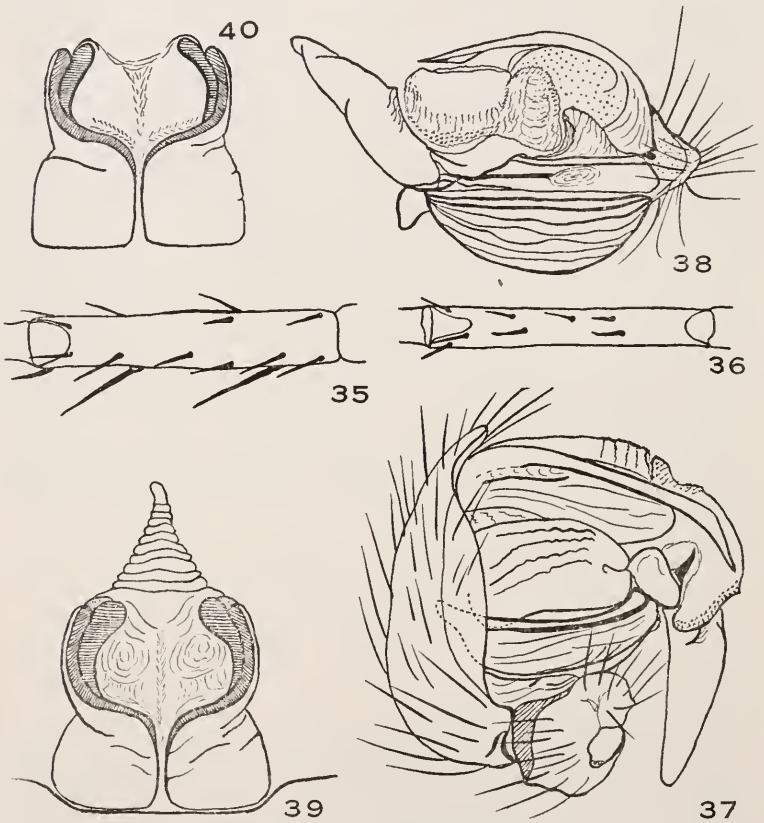
(Figures 35-40)

Epeira bifida Banks, 1909
Eustala bifida Petrunkevitch, 1911

As indicated in the treatment of *E. maxima* sp. nov., the females reported by Banks (1929) from Barro Colorado Island are now regarded as belonging to a species new to science. The specimens in the Museum of Comparative Zoology from La Verbena, Costa Rica, agree well with the specimens from the British Museum and with F. P. Cambridge's figures. All of the specimens from La Verbena are somewhat shrunken and distorted but are, nevertheless, easily identified.

Male hypotype. Total length 6.175 mm. The hypotype has the bifid condition at the posterior end of the abdomen but in a reduced degree. Central ocular quadrangle wider in front than

behind in ratio of 7 : 6 only slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 13 : 8 : 12 : 7.5. AME separated from one another by 1.5 times their diameter, from ALE by about 2.5 times their diameter. PME separated from



External Anatomy of *Eustala*
Figures 35-40, *E. bifida*

Fig. 35. Left second tibia from below.
Fig. 36. Right fourth femur from below.
Fig. 37. Left male palpal tarsus, lateral view.
Fig. 38. Left male palpal tarsus from in front.
Fig. 39. Epigynum from below.
Fig. 40. Epigynum; a more posterior view.

one another by 1.25 times their diameter, from PLE by about four times their diameter. Laterals separated from one another by about the diameter of ALE. Height of clypeus equal to slightly more than 1.5 times the diameter of AME. Promargin of fang groove with four teeth, second and fourth smaller than first and third; retromargin with three rather small teeth. Secondary sexual characters appear about as usual except that the ridge and groove on the promargin of the second femur is much shorter than usual.

Legs. 1243. Width of first patella at "knee" .455 mm., tibial index of first leg 9. Width of fourth patella at "knee" .444 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.225	1.690	3.477	3.600	[1]1.300	14.292
2.	3.445	1.430	2.665	3.250	[1]1.225	12.015
3.	2.535	.975	1.365	1.570	.845	7.290
4.	3.185	1.495	2.405	2.730	1.105	9.920
Palp	.498	.249	.238	——	1.029	2.014

The special ventral and prolateral spines on the second tibia are shown in Figure 35. The first femur has a double series of ventral spines apparently with three on the promargin and three or four on the retromargin, all in distal half. The second femur is essentially like the first in this respect. The third femur has one or two ventral spines on the promargin and three on the retromargin. The fourth femur has the most fully developed set of ventral spines with four on each margin (Fig. 36).

Palp. In very close agreement with the specimen from the British Museum. The features of the femur, patella, and tibia appear to be typical of the genus. Tarsus: basal tarsal apophysis is typical; the clavis is robust, unexcavated at base but with a short ridge as noted by F. P. Cambridge; the uncus has a transversely inflated base from which the point of the hook extends but there is no long shank; the conductor is massive, extensively setose, with a ventral depression for the reception of the point of the uncus, and with two characteristic surfaces at the distal end, one of which has a shallow groove; the vesicle is of moderate size but is well defined; the embolus is long, slender,

[1] Lacking in hypotype; length estimated.

and terminally lance-like; the terminal laminae are massive in the medial half and bear two poorly defined grooves in the reduced retrolateral half (Figs. 37-38).

Color in alcohol. Discolored by long preservation and, probably also, by drying out at some time. The dorsal folium was probably well defined. In all available specimens the venter has a somewhat elongated light spot in the center of what was probably a dark area behind the genital groove.

Female hypotype. Total length about 7.475 mm. (distorted and difficult to measure accurately). The bifid condition of the posterior end of the abdomen is fairly conspicuous in spite of the distortion.

Legs. 1243. Width of first patella at "knee" .601 mm., tibial index of first leg 11. Width of fourth patella at "knee" .585 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.225	1.950	3.575	3.380	1.365	14.495
2.	3.705	1.885	3.055	3.250	1.235	13.130
3.	2.600	1.105	1.495	1.690	.975	7.865
4.	3.640	1.820	2.697	2.925	1.105	12.187

There is a double series of weak ventral spines on the first femur, three on promargin and two on retromargin, all in distal half; there are also three prolateral femoral spines the first two of which are long and robust, all in distal half. The ventral femoral spines appear to be lacking on the second leg but the prolateral spines are three in number and all weak. The third and fourth femora appear to lack the ventral spines.

Epigynum. Similar to that of *E. maxima* sp. nov. There are quite definite though somewhat obscure differences in the pattern of tubules and their boldness together with the prominences in the expanded region from which the scape arises. These are best shown in Figures 39-40.

Type locality. F. P. Cambridge had this species only from Costa Rica. The only specimens available to me for study are also restricted to Costa Rica. The hypotypes and two other female specimens are from La Verbena, collected in January by Tristan and now a part of the Nathan Banks collection in the Museum of Comparative Zoology.

Eustala bucolica sp. nov.

(Figures 41-44)

Male holotype. Total length 3.835 mm. Carapace 1.982 mm. long; 1.755 mm. wide opposite third coxae where it is widest; .845 mm. tall and, therefore, about .48 as tall as wide; rises gradually from PME to beginning of steep posterior declivity opposite third coxae; with well developed median longitudinal thoracic groove; with no more than a weak covering of hair and with few spines or spinules and these confined to ocular area.

Eyes. As usual, eight in two rows, all dark; LE on moderately prominent tubercles; viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of about 8 : 7, wider in front than long in ratio of about 16 : 15. Ratio of eyes AME : ALE : PME : PLE = 10 : 7 : 9 : 7. AME separated from one another by 1.5 times their diameter, from ALE by the same distance. PME separated from one another by 1.25 times their diameter, from PLE by three times their diameter. Laterals separated from one another by about two-thirds of their diameter. Height of clypeus equal to the diameter of AME.

Chelicerae. Basal segment .758 mm. long. Fang groove well defined and finely dentated; promargin with four teeth, the second and fourth smaller; retromargin with three teeth (observed on paratype to avoid injury to holotype). Otherwise as usual in the genus.

Maxillae. As usual in the genus in all observed features including the maxillary tooth which appears to be used in opposition to the basal palpal femoral ridge.

Lip. Wider than long in ratio of about 25 : 16; transversely grooved in proximal half; reaches to about the middle of maxillae. Sternal suture gently procurved.

Sternum. Scutiform; longer than wide in ratio of 7 : 6; a narrow sclerite continues between fourth coxae which are separated by about one-third of their width; with the usual supply of long slender spinules.

Legs. 1243. Width of first patella at "knee" .282 mm., tibial index of first leg 8. Width of fourth patella at "knee" .217 mm., tibial index of fourth leg 10.

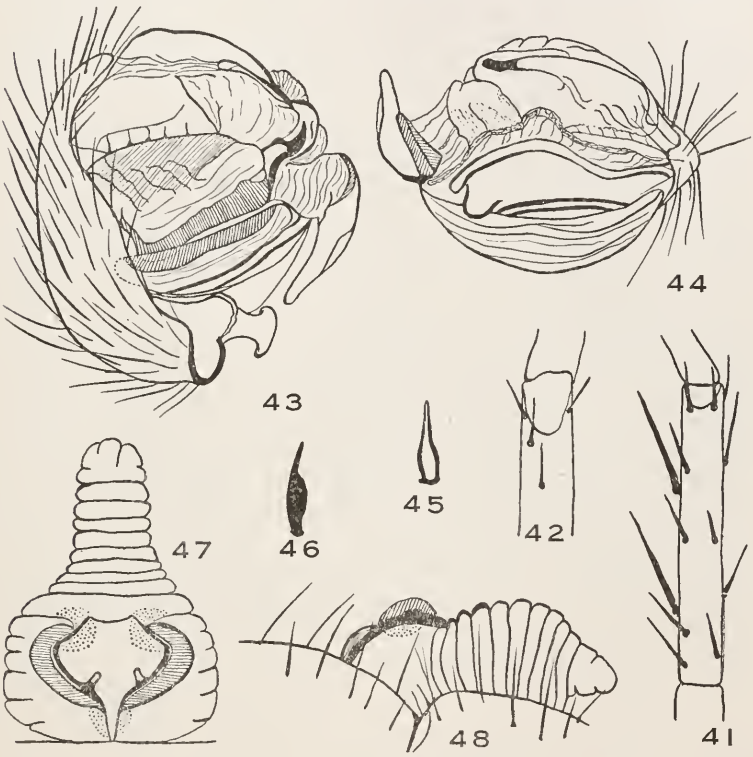
	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.990	1.012	2.405	2.156	.902	9.465
2.	2.200	.836	1.650	1.738	.792	7.216
3.	1.430	.550	.748	.770	.484	3.932
4.	1.980	.792	1.298	1.320	.616	6.006
Palp	.352	.220	.176	——	.704	1.452

The hook and tubercle on the first coxa and the ridge and groove on the second femur appear to be typical of the genus.

Spines. First leg: femur dorsal 0-1-1-1, prolateral left 0-1-1-1-1, right 0-0-1-1-1, retrolateral 0-0-1-1-1, ventral promargin 0-1-0-0-0 and retromargin 0-0-1-1; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 0-1-0-0-1-1-0, prolateral 0-1-0-1-0, retrolateral 0-1-1-0, ventral 2-lr-lp-lr-lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0, retrolateral 0-1-0-1-0, ventral 0-2-lp-0. Second leg: femur dorsal and prolateral 0-1-1-1, retrolateral the same with slight variations, ventral only one on each margin near distal end; patella dorsal as in first, prolateral 1-1, retrolateral as in first; tibia dorsal 1-0-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-lp-2-lp-2 (Fig. 41); metatarsus dorsal 0-1-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-2-lp-0. Third leg: femur dorsal 0-1-1-1, prolateral 0-0-1-1, retrolateral only one near distal end, ventral only two on promargin and one near distal end on retromargin; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-0-1, prolateral 1-1-0, retrolateral 0-1-0, ventral lp-lp-2; metatarsus dorsal and prolateral 0-1-0-0, retrolateral 0-1-0, ventral lp-lp-lp-lp(weak). Fourth leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral promargin only one near distal end and three along retromargin, all in distal half (Fig. 42); patella as in third; tibia dorsal 1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-1, ventral 2-lp-lp-2; metatarsus dorsal 1-1-0, prolateral 1-1-1-1, retrolateral 0, ventral 0-lp-lp-lp(weak).

Palp. Complicated; basal femoral ventral ridge, patella, and tibia typical of the genus. Tarsus: basal tarsal apophysis a typical distorted arrow-head shape; the clavis is moderately robust, somewhat concave ventrally at its base and provided with a marked carina along its basal lateral border; the uncus is a stout hook with a pronounced shoulder at its base; the conductor

is relatively small, less differentiated on its anterior surface than usual and only sparsely and very finely setose; the vesicle is in its typical position and of moderate size; the free part of the embolus is short and slender but its base extends nearly to



External Anatomy of *Eustala*
Figures 41-44, *E. bucolica* sp. nov.
Figures 45-48, *E. clavispina*

Fig. 41. Left second tibia from below.
Fig. 42. Right fourth femur from below.
Fig. 43. Left male palpal tarsus, lateral view.
Fig. 44. Left male palpal tarsus from in front.
Figs. 45-46. Two views of claviform abdominal spines.
Fig. 47. Epigynum from below.
Fig. 48. Epigynum, lateral view.

the border of the bulb; the terminal laminae are only moderately wrinkled but there is a very prominent tubercle present together with a large raised portion contiguous to the base of the conductor (Figs. 43-44).

Abdomen. Total length 2.275 mm.; 1.625 mm. wide; with the typical round-triangular form; with the usual long slender dorsal and dorsolateral spinules; other observed features typical of the genus.

Color in alcohol. Carapace yellowish with grayish flecks over the anterior half; a transverse row of four small brownish dots across near the posterior end of the thoracic groove and another transverse row of two dots near the anterior end of the groove. Sternum yellowish with a grayish margin. Legs as usual, yellowish with brownish spots, bars, and rings. Abdomen: with a well developed dorsal folium subject to many variations among paratypes; the holotype has a conspicuous round, central, deeply colored, brown spot just in front of the middle of the folium but this is not persistent among the paratypes; the venter has a dark quadrilateral area between the genital groove and the base of the spinnerets and this has a very narrow dark lateral border enclosing a curved light colored mark on each side ending in a small posterior whitish spot but these are all subject to much variation among the paratypes.

Type locality. The holotype male is from Boquete, R. P., August, 1939. Several male paratypes from the same locality, August, 1939, 1950; one male paratype from El Volcan, R. P., February, 1936 (W. J. Gertsch).

Eustala clavispina (O. P. Cambridge), 1889

(Figures 45-48)

Epeira clavispina O. P. Cambridge, 1889
E. clavispina Keyserling, 1892
Amamra nigromaculata O. P. Cambridge, 1895
Eustala clavispina F. P. Cambridge, 1904
E. clavispina Petrunkevitch, 1911

This species has not yet appeared in my collection nor has it been found in any of the material loaned me from the American Museum or available for study in the Museum of Compara-

tive Zoology. The only specimens I have seen are those loaned from the British Museum. These have enabled me, however, to form a clear conception of the female of the species. One of these females has been made the source of the following data and thus becomes the hypotype.

Female hypotype. Total length 6.467 mm. The abdomen shows a slight tendency to be bilobed at its base and is quite distinctly bifid at its posterior end as in *E. bifida.* There is also a distinct low cone in the area enclosed by the central ocular quadrangle; above and medial to ALE there is also a distinct convexity. The central ocular quadrangle is almost as wide behind as in front; slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 10 : 7.5 : 11 : 8.5. AME separated from one another by 1.5 times their diameter, from ALE by about three times their diameter. PME separated from one another a little more than their diameter, from PLE by a little more than four times their diameter. Laterals separated from one another by the diameter of PLE. Height of clypeus equal to a little less than twice the diameter of AME. Promargin of fang groove with four teeth, the second and fourth the smallest; retromargin with three teeth. Perhaps the most distinctive feature of this species is the curious type of spinule common on the dorsal and dorsolateral parts of the abdomen and on at least certain segments of the legs (Figs. 45-46). A pair of these unusual spinules also occurs on the tip of the low ocular cone in central ocular quadrangle.

Legs. 1243. Width of first patella at "knee" .401 mm., tibial index of first leg 10. Width of fourth patella at "knee" .368 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.185	1.462	2.730	2.600	1.040	11.017
2.	2.795	1.300	2.275	2.340	.975	9.685
3.	1.852	.715	1.007	1.170	.715	5.459
4.	2.600	1.365	1.755	2.015	.780	8.515

Ventral femoral spines are few or lacking; the first femur has a pair of slender spinules in the position 0-lr-lr-0; the second femur has a similar series of four as follows: lr-lr-lr-lr-0.

Epigynum. Base with the usual general pattern of tubules,

apertures, and striations; the base is relatively broad and massive (Figs. 47-48).

Color in alcohol. The dorsum of the abdomen is clay-yellow with a poorly defined folium; laterally there is a series of narrow brownish bands rising from the venter and ending dorsolaterally in brownish lines; these latter alternate with whitish bands from the dorsum which point ventrally; the venter is sprinkled with whitish granules concentrated toward the center between the genital groove and base of the spinnerets.

Type locality. The hypotype is from Teapa, Tabasco, Mexico (H. H. Smith), included among three specimens from the British Museum from the Godman and Salvin collection, April, 1905. F. P. Cambridge had specimens from Mexico and Guatemala.

Eustala conformans Chamberlin, 1925

(Figures 49-50)

E. conformans Banks, 1929

Banks (1929) had doubts about the validity of this species but, after a careful study of the holotype female, I am forced to accept it as a true species. All of my specimens referred to this species are considerably larger than the holotype but the epigyna agree remarkably well. I have, therefore, little doubt of the accuracy of the identification.

Female hypotype. Total length 6.175 mm. The general structure appears to be quite typical of the genus; there is a slight convexity between AME and PME from which a pair of slender spines extend; the carapace is covered by a well developed coat of whitish hair, raised into a tuft behind the LE; there is barely a suggestion of shoulder humps; the leg spines appear to be developed as usual in the genus. The central ocular quadrangle is only slightly wider in front than behind and only slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 11.5 : 9 : 11 : 8. AME separated from one another by about 1.2 times their diameter, from ALE by twice their diameter. PME separated from one another 1.3 times their diameter, from PLE by a little less than four times their diameter. Laterals separated from one another by two-thirds of the diameter of ALE. Height of clypeus equal to 1.3

times the diameter of AME. Promargin of fang groove with the usual four teeth and the retromargin with three teeth.

Legs. 1243. Width of first patella at "knee" .390 mm., tibial index of first leg 11. Width of fourth patella at "knee" .379 mm., tibial index of fourth leg 14.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.665	1.300	2.210	2.080	.910	9.165
2.	2.567	1.170	1.885	1.917	.877	8.416
3.	1.690	.585	.845	1.100	.660	4.880
4.	2.600	1.170	1.630	1.852	.845	8.097

Ventral spines appear to be completely lacking from the femora.

Epigynum. Somewhat resembles that of *E. semifoliata* but it is relatively broader and shorter; the apertures are much closer together than in *E. semifoliata;* there is a large dark area on each side of the base, not noted in any other species (Figs. 49-50).

Color in alcohol. Carapace yellowish with no dots or spots such as so frequently occur. Sternum yellowish with a grayish margin. The legs are yellowish with a few brown bars and spots. Abdomen: the dorsal folium is almost completely lacking with the dorsal and dorsolateral regions yellowish white from numerous subchitinous granules; the venter has a large area between the genital groove and base of spinnerets outlined irregularly with a white margin and containing a somewhat aviform black figure; this ventral pattern appears quite constant in all specimens recently collected but there is great variation among these in respect to other color features.

Type locality. The hypotype is from the Barro Colorado Island, C. Z., May, 1946 (Schnierla). Four other specimens from the same locality are in the collection: February, 1936 (Gertsch); May, 1946 (Schnierla); July, 1950.

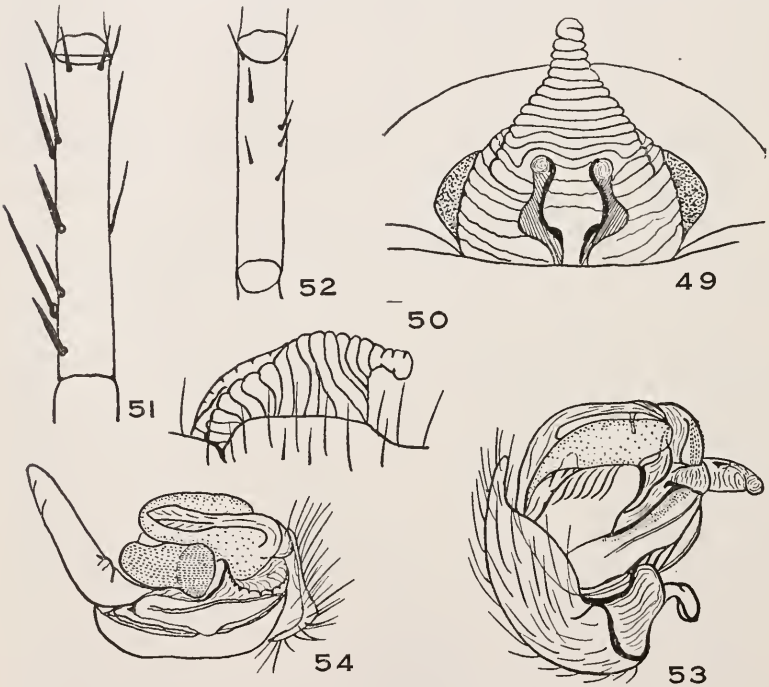
Eustala delecta sp. nov.

(Figures 51-54)

Male holotype. Total length 5.330 mm. Carapace 2.535 mm. long; 2.210 mm. wide opposite interval between second and third coxae; .845 mm. tall and, therefore, about .38 as tall as wide;

rises gently from PME to beginning of steep posterior declivity; with well developed median thoracic groove; with spines apparently confined to the ocular area.

Eyes. As usual, eight in two rows, all dark; LE on moderately prominent tubercles, viewed from above, posterior row moderately recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider



External Anatomy of *Eustala*
Figures 49-50, *E. conformans*
Figures 51-54, *E. delecta* sp. nov.

Fig. 49. Epigynum from below.
Fig. 50. Epigynum, lateral view.
Fig. 51. Left second tibia from below.
Fig. 52. Left fourth femur from below.
Fig. 53. Left male palpal tarsus, lateral view.
Fig. 54. Left male palpal tarsus from in front.

in front than behind in ratio of 44 : 39, wider in front than long in the same ratio. Ratio of eyes AME : ALE : PME : PLE = 13 : 8 : 11 : 9. AME separated from one another by about 1.66 times their diameter, from ALE by a little less than twice their diameter. PME separated from one another by about 1.7 times their diameter, from PLE by a little less than four times their diameter. Laterals separated from one another by nearly three-fourths of the diameter of ALE. Height of clypeus equal to 1.15 times the diameter of AME.

Chelicerae. Basal segment .747 mm. long. Fang groove well defined; apparently with four teeth on promargin and three on retromargin as usual. Otherwise essentially typical of the genus.

Maxillae. In general quite typical of the genus including the maxillary tubercle used in opposition to the palpal femoral ridge.

Lip. Wider than long in ratio of about 4 : 3; hence somewhat narrower than usual in the genus; reaches to about the middle of the maxillae. Sternal suture difficult to see but apparently somewhat procurved.

Sternum. Scutiform; longer than wide in ratio of about 9 : 7; a narrow sclerite continues between the fourth coxae which are barely separated; with the usual covering of stiff bristles.

Legs. 1243. Width of first patella at "knee" .368 mm., tibial index of first leg 9. Width of fourth patella at "knee" .325 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.575	1.170	3.055	2.892	1.137	11.829
2.	2.762	1.170	2.210	2.600	1.040	9.782
3.	2.015	.812	1.040	1.235	.715	5.817
4.	2.600	1.137	1.722	2.210	.788	8.454
Palp	.596	.260	.238	——	.823	1.917

First coxa with the usual well developed ventral distal retrolateral hook and the dorsal tubercle; the prolateral groove and ridge on the second femur well developed.

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral 0-0-2-1-1, retrolateral 0-0-0-1-1, ventral a single series of five on retromargin 0-0-1-1-1-1-0-1; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral 0-1-0-1-0, retrolateral 0-1-0-1-1, ventral 2-lp-lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0, retrolateral 0-1-1-0, ventral 2-2(irregular)-

lp-0. Second leg: femur dorsal as in first, prolateral and retrolateral 0-0-0-1-1, ventral with a double series, five along retromargin and two on promargin in distal quarter; patella as in first; tibia dorsal 0-1-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-0-1-1-1, ventral lp-lp-lp-lp-2 (Fig. 51); metatarsus dorsal 0-1-1-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-2-lp-0. Third leg: femur dorsal as in first, prolateral and retrolateral only one near distal end, ventral only two on retromargin in distal third; patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 0-1-0-1-0, prolateral 1-1-1, retrolateral 0-0-1-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral and retrolateral 0-1-0, ventral 1-1-1-1. Fourth leg: femur dorsal as in first, prolateral and retrolateral apparently only one near distal end, ventral four on retromargin in distal two thirds and three on promargin in distal half (Fig. 52); patella as in third; tibia dorsal 0-1-1-1-0, prolateral 1-1-1-1, retrolateral 1-1-1, ventral 2-lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0-1-1-0, retrolateral 0-0-1-1-0, ventral 0-1-1-1.

Palp. Complicated; basal femoral tubercle or ridge opposing maxillary tooth moderately well developed; patella short with a weak proximal dorsal spine and a long slender distal dorsal spine as usual; tibia also short, trilobed, and with the usual chitinized rim or collar on the articular lobe together with a less conspicuous dorsal rim. Tarsus: the basal apophysis is a distorted arrowhead shape; the clavis is robust and projects ventrally more than usual in the genus; the uncus is a somewhat twisted spine lying in a depression in the conductor largely made by a small marginal lobe of the latter; the conductor is relatively large, with a small marginal lobe somewhat like that of *E. scutigera* and two characteristic anterior surfaces both of which are finely setose and with the smaller surface somewhat concave; the vesicle is moderately large; the embolus is of moderate length, relatively broad and flat; the terminal laminae are only moderately wrinkled and striated but are concave and massive contiguous to the conductor (Figs. 53-54).

Abdomen. 3.12 mm. long; 2.275 mm. wide about one-third from base where it is widest; with the usual supply of long slender spinules; other observed features appear to be typical of the genus.

Color in alcohol. Carapace shows no dots but the paratypes show that these may be present in certain individuals; when present they appear as a transverse row of four at level of middle of thoracic groove; the holotype shows a large pale brownish spot on each side at anterior end of thoracic groove and this appears to be more or less constant among the paratypes; the area behind LE is flecked with gray. Sternum yellowish with gray flecks around the margin. Legs are yellowish with broad brownish rings together with pale and darker spots. Abdomen: the dorsal folium is well developed; the venter has the usual darker area between genital groove and base of spinnerets containing a central granular oval white spot but the white mark is variable among the paratypes.

Type locality. The holotype is from Barro Colorado Island, C. Z., August, 1936. Six paratype males have been found in my collections from the following localities: Barro Colorado Island, August, 1936; July-August, 1939; July, 1950; Summit, C. Z., July, 1950; Boquete, R. P., August, 1950.

Eustala exigua sp. nov.

(Figures 55-58)

Male holotype. Total length 3.315 mm. Carapace 1.69 mm. long; 1.386 mm. wide opposite interval between second and third coxae where it is widest; with shape typical of the genus; with a moderately well developed coat of light and dark hair; with numerous long slender spines in ocular area and two pairs of spinules just in front of the well developed median longitudinal thoracic groove; .638 mm. tall opposite third coxae and, therefore, about .46 as tall as wide.

Eyes. Eight in two rows, all dark. Viewed from above, posterior row gently recurved; viewed from in front, anterior row straight. Anterior row nearly as wide as posterior row. Ratio of eyes AME : ALE : PME : PLE = 12: 8.5 : 9 : 7.5. AME separated from one another by their diameter, from ALE by three-fourths of their diameter. PME separated from one another by five-sixths of their diameter, from PLE by about five-halves of their diameter. Laterals separated from one another by one-third of the diameter of PLE. Central ocular quadrangle

wider in front than behind in ratio of 4 : 3, only slightly wider in front than long. Height of clypeus equal to a little less than three-fourths of the diameter of AME.

Chelicerae. Moderately robust; essentially parallel; basal segment .55 mm. long; with a moderately well developed basal boss. Promargin of fang groove with four teeth; retromargin with four small teeth, one of which is minute (teeth determined from a paratype to avoid injury to the holotype). With well developed scopulae.

Maxillae. Slightly convergent; normal to the genus; with the tubercle well developed in opposition to the palpal femoral ridge.

Lip. Wider than long in ratio of 13 : 8; maxillae extend beyond lip to a distance equal to three-fourths of its length. Sternal suture moderately procurved.

Sternum. Scutiform; moderately convex; widest between second coxae; longer than wide in ratio of 31 : 29; sternum proper not extended between fourth coxae but a narrow sclerite continues posteriorly between fourth coxae which are separated by about one-third of their width.

Legs. 1243. Width of first patella at "knee" .249 mm., tibial index of first leg 8. Width of fourth patella at "knee" .206 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.530	.836	2.222	1.936	.792	8.316
2.	1.760	.660	1.430	1.606	.660	6.116
3.	1.166	.396	.638	.726	.440	3.366
4.	1.716	.616	1.188	1.364	.550	5.434
Palp	.352	.132	.154	——	.594	1.232

Spines. First leg: femur dorsal 0-1-1-0-1-1, prolateral 0-1-1-1-1, retrolateral 0-0-0-0-1-1, ventral a double series with two on promargin and four on retromargin and all near middle; patella dorsal 1(weak)-1, prolateral and retrolateral 1-1; tibia dorsal 0-1-0-1-0 on right and 0-1-0-1-1-0 on left, prolateral 0-1-0-1-1, retrolateral 0-1-1-0, ventral 2-2-2 with irregularities between right and left; metatarsus dorsal 1-1-0-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-2-0-0. Second leg: femur dorsal essentially as in first, prolateral only one near distal end, retrolateral 0-0-0-1-1, ventral with no true spines on promargin but with an

irregular series of five on retromargin and stiff bristles which suggest additional reduced spines; patella dorsal as in first, prolateral 1-0, retrolateral 1-1; tibia dorsal 1-1-1-0, prolateral 1-1-1-0-1, retrolateral 0-1-1-0, ventral 0-0-1-2 (Fig. 55); metatarsus dorsal 1-1-1-0-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-2-0-0. Third leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral with four robust spines on left and five on right and more or less medial in position; patella only dorsal 1-1; tibia dorsa 0-1-0-1-0, prolateral 0, retrolateral 0-1-1, ventral 0-lp-2; metatarsus dorsal 1-0-0, prolateral and retrolateral 0-1-0, ventral 0-lp-2. Fourth leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral a double series of eleven on left and seven on right, irregularly placed (Fig. 56); patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-1-1-0, prolateral 0-1-1-1, retrolateral 0-1-1, ventral 0-0-lp-2; metatarsus dorsal 1-1-0, prolateral 0-1-1-1, retrolateral 0, ventral 0-0-2. Numerous variations of spination have been noted among the paratypes and even from side to side in the holotype. Palp: patella dorsal 1(weak)-1(long, slender); tibia with numerous bristles some of which might be considered slender spines; tarsus with numerous stiff bristles. First coxa with the usual hook at the distal retrolateral corner. Second femur with the usual chitinized ridge and groove on the prolateral side.

Palp. Trochanter with a low, relatively large, chitinous tubercle; femur with a basal curved chitinous ridge; patella with a single long dorsal distal spine. The tibia is trilobate as follows: dorsal lobe triangular with a ruffled chitinized anterior margin; the body has a ventral chitinized rim and a strongly chitinized prolateral tubercle; the retrolateral lobe is rounded and less chitinized. Tarsus: the basal apophysis is a strongly chitinized, modified arrow-shaped structure; the clavis is somewhat excavated at its base and is moderately robust; the uncus is a relatively long slender spine which appears distally bifid; the conductor is relatively large, with an excavated distal border, and has two slender apophyses extending from its median rim; the vesicle is large for so small an organ and has an unusual terminal position; the embolus is broad at its base and tapers to a point after passing around the vesicle in an unusual manner; the

terminal laminae show a pair of low grooves distally placed (Figs. 57-58).

Abdomen. Total length 1.885 mm.; with the usual rounded triangular form; longer than wide in ratio of about 5 : 2; with the usual supply of long slender spines; with other features essentially typical of the genus.

Color in alcohol. As usual the color pattern in this species is highly variable and, as commonly used, of little value in determination of the species. The holotype has a well defined dorsal folium with a hexagonal dark spot at its anterior end but the folium itself is highly variable in the different available specimens and sometimes almost lacking. The median anterior dark spot seems to be the most persistent part of the folium. There is a transverse row of four small dots across the carapace near the posterior end of the thoracic groove and a dark spot of irregular shape on each side of the pars cephalica with a white spot between. The holotype has a ventral triangular dark spot with its apex at the base of the spinnerets without the usual central white spot but the latter appears in some paratypes. The sternum is yellowish with dark marginal flecks.

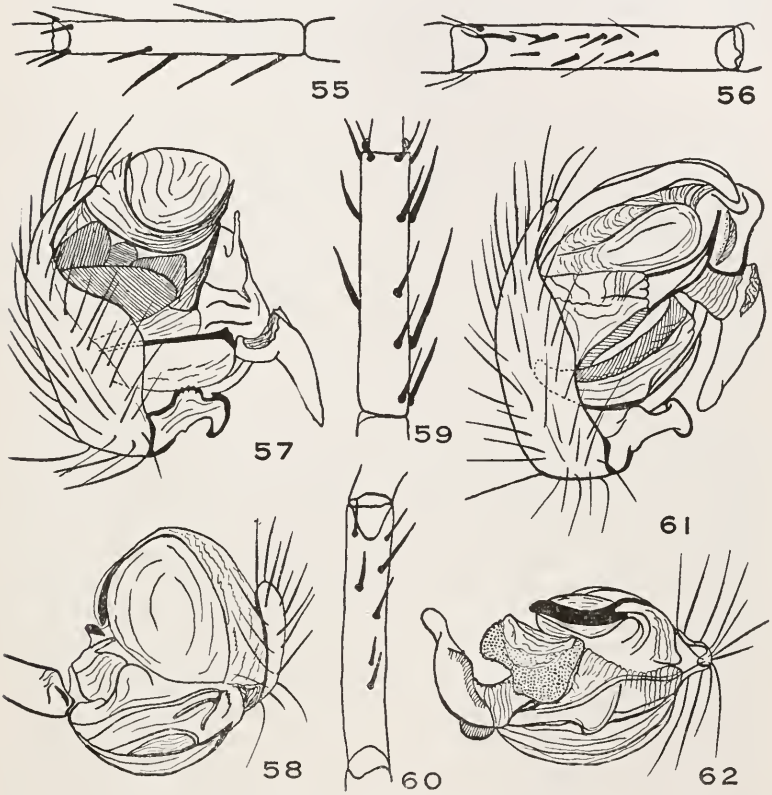
Type locality. Male holotype from Barro Colorado Island, C. Z., July, 1939. Numerous male paratypes from the following localities: Barro Colorado Island, July-August, 1936; July-August, 1939; June-July, 1950; Ft. Sherman, C. Z., August, 1939; Canal Zone Forest Reserve, C. Z., August, 1936 and July-August, 1939; El Valle, R. P., July, 1936; Arraijan, R. P., July, 1950.

Eustala fragilis (O. P. Cambridge), 1889

Epeira fragilis O. P. Cambridge, 1889
E. fragilis Keyserling, 1892
Eustala fragilis F. P. Cambridge, 1904
E. fragilis Petrunkevitch, 1911
E. fragilis Petrunkevitch, 1925

The Cambridges had this species from Guatemala and Panama but the British Museum (Natural History) was unable to loan me any representative. Until recently I have regarded the species treated in this paper as *E. minima* sp. nov. as *E. fragilis* (O. P. Cambridge) but at the present time I am unable to do this. I am also unable to work out any clear understanding of

the species from published statements concerning it. I am, therefore, compelled to omit the species from the keys and to leave its



External Anatomy of *Eustala*
Figures 55-58, *E. exigua* sp. nov.
Figures 59-62, *E. gertschi* sp. nov.

Fig. 55. Left second tibia from below.
Fig. 56. Left fourth femur from below.
Fig. 57. Left male palpal tarsus, lateral view.
Fig. 58. Left male palpal tarsus from in front.
Fig. 59. Right second tibia from below.
Fig. 60. Left fourth femur from below.
Fig. 61. Left male palpal tarsus, lateral view.
Fig. 62. Left male palpal tarsus from in front.

proper treatment until a more thorough understanding of it is obtained.

Eustala gertschi sp. nov.

(Figures 59-62)

Male holotype. Total length 4.452 mm. Carapace 2.405 mm. long; 1.950 mm. wide opposite interval between second and third coxae where it is widest; .845 mm. tall and, therefore, about .43 as tall as wide; gently inclined from PME to beginning of steep posterior declivity; median longitudinal thoracic groove well developed; with a distinct but low convexity between AME and PME from which two long slender spines extend; with a well developed coat of whitish procumbent hair extended into a distinct tuft dorsal and posterior to LE.

Eyes. As usual, eight in two rows, all dark; LE on moderately prominent tubercles; viewed from above, posterior row distinctly recurved; viewed from in front and measured by centers, anterior row gently procurved; central ocular quadrangle only slightly wider in front than behind and only slightly longer than wide in front. Ratio of eyes AME : ALE : PME : PLE = 12 : 8 : 10 : 8. AME separated from one another by nine-eighths of their diameter, from ALE by five-thirds of their diameter. PME separated from one another by seven-fifths of their diameter, from PLE by seven-halves of their diameter. Laterals separated from one another by one-half of their diameter. Height of clypeus equal to three-halves of the diameter of AME.

Chelicerae. Basal segment .596 mm. long. Fang groove well defined; promargin with the usual four teeth and retromargin with three but these seem smaller and less clearly defined than usual (observed on a paratype to avoid injury to the holotype). Otherwise typical in all observed features.

Maxillae. As usual in the genus in all observed features including the maxillary tooth used in opposition to the palpal femoral ridge.

Lip. Wider than long in ratio of 35 : 22; moderately grooved and striated in basal third. Sternal suture definitely procurved.

Sternum. Scutiform; longer than wide in ratio of about 9 : 7; a narrow sclerite continues between fourth coxae which are

separated by about one-seventh of their width; moderately convex; markedly scalloped opposite all coxae except the fourth and with narrow sclerites continuing between all coxae.

Legs. 1243. Width of first patella at "knee" .347 mm., tibial index of first leg 12. Width of fourth patella at "knee" .314 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.535	1.040	1.885	1.852	.942	8.254
2.	2.015	.910	1.657	1.787	.845	7.214
3.	1.495	.528	.770	.924	.594	4.311
4.	2.080	.910	1.560	1.848	.814	7.212
Palp	.425	.220	.180	——	.946	1.771

First coxa with the usual ventral hook and dorsal tubercle, both well developed; ridge and groove on second femur also well developed as usual.

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral 0-0-1-1 (both robust)-1 on right and 0-0-1-1-1-1 on left, retrolateral 0-0-0-1-1, ventral 0; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral lp-lp-lp-lp-2; metatarsus dorsal 1-0-1-0, prolateral 0, retrolateral 0-1-0-0, ventral 0-2-2-lr-0. Second leg: femur dorsal as in first, prolateral and retrolateral 0-0-0-1-1, ventral 0; patella as in first except prolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral 1-1-0-1-1, retrolateral 0-1-1-1, ventral lp-lp-lp-lp-2 (Fig. 59); metatarsus dorsal 0-1-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-2-2-lp. Third leg: femur dorsal 0-1-0-1, prolateral and retrolateral only one near distal end, ventral three on retromargin; patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 0-1-0-1-0, prolateral 1-1-1, retrolateral 0-1-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-0-1, retrolateral 0-1-0, ventral 0-1-0-1. Fourth leg: femur dorsal 0-1-0-1-1, prolateral and retrolateral only one near distal end, ventral two on promargin in distal fourth and five on retromargin in distal two-thirds of segment (Fig. 60); patella as in third; tibia dorsal 0-1-1-1-0, prolateral 1-1-0-1-0, retrolateral 0-1-1, ventral lp-2-lp-2; metatarsus dorsal 1-1-0-1-0, prolateral 0-1-0-1-1, retrolateral 0, ventral lp-lp-0-lp-lp.

Palp. Complicated; femur, patella and tibia all apparently

typical of the genus. Tarsus: basal apophysis well developed as usual but its distal end is simply bent and knobbed, not a distorted arrow-head as is typically the case; the clavis is moderately robust and somewhat excavated at its base and also has a characteristic ridge and groove on the anterior surface of the proximal part of the free portion; the uncus is very long, slender, curved, and apparently finely divided at its distal end; the conductor is large and quadrilateral in outline as usually viewed; there is also a fold and a depression on the ventral surface of the conductor contiguous to the tip of the uncus which gives the appearance of a distinct lobe in one of the paratypes; the anterior end of the conductor is differentiated into an extensive setose surface and a small smooth portion; in one paratype the anterior surface of the conductor shows a shallow depression; the vesicle is rather smaller than average but definite and in its usual position; the embolus is long and somewhat sinuous, robust and somewhat flattened; the terminal laminae show a prominent elevation contiguous to the conductor and a large blunt tubercle (Figs. 61-62).

Abdomen. Rather oval in outline; 2.470 mm. long; 2.242 mm. wide; somewhat flattened dorsoventrally; with the usual supply of dorsal and dorsolateral long slender spinules. With other observed features typical of the genus.

Color in alcohol. Carapace: ocular area yellowish; remainder of pars cephalica brownish; lateral sides of pars thoracica brown with dorsal parts lighter and mottled. Sternum grayish with white subchitinous granular spots. Legs: all femora dark brown dorsally, lighter beneath; other segments yellowish with brownish spots. Abdomen: with a moderately well developed narrow dorsal folium; white or grayish from subchitinous granules elsewhere dorsally, dorsolaterally and laterally; venter with the usual dark central area containing a small central white spot. The paratype collected by Dr. Gertsch is without a folium and is much lighter throughout.

Type locality. Male holotype from Barro Colorado Island, C. Z., June, 1950. Two male paratypes from the same locality; February, 1936 (Gertsch) and June, 1948 (Schneirla).

Eustala guttata F. P. Cambridge, 1904
(Figures 63-68)

E. guttata Petrunkevitch, 1911

E. guttata Petrunkevitch, 1925
E. guttata Banks, 1929 (female but not male)

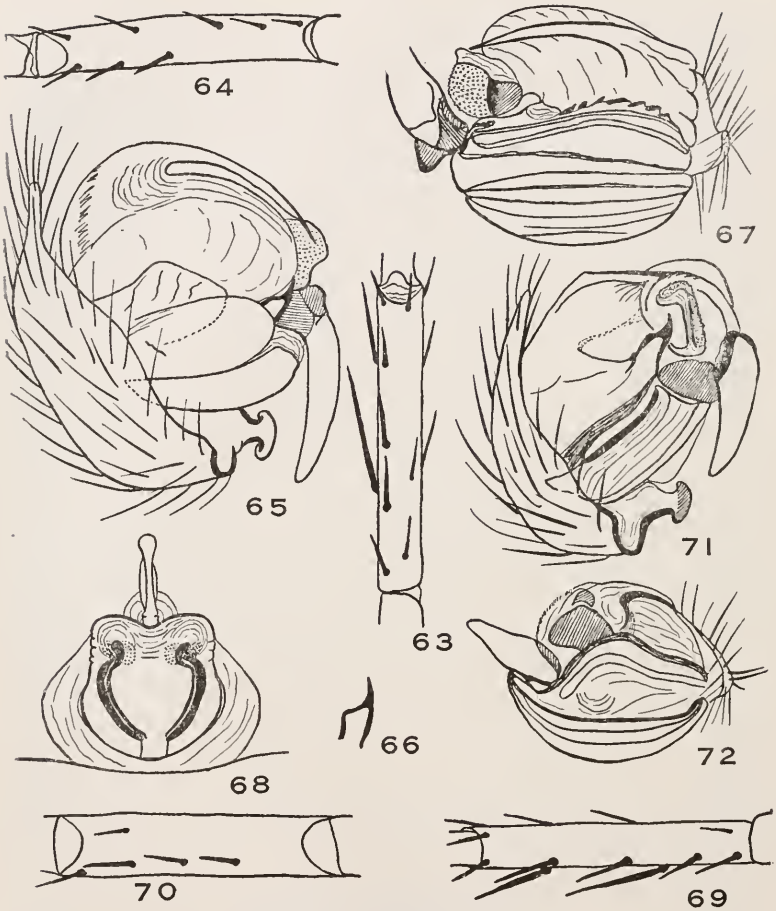
I have found it difficult to identify the males of this species. The two male specimens on loan from the British Museum (Natural History) differ considerably from one another. I have chosen as my standard the one which agrees most fully with F. P. Cambridge's description and figures. I have also included in the species as now recognized a few males which appear to be deviates from the typical. The females appear to be endowed with characters sufficiently distinctive to make their identification relatively simple.

Male hypotype. Total length 4.225 mm. With the usual round triangular form of the body. Central ocular quadrangle wider in front than behind in ratio of about 4 : 3, wider in front than long in ratio of about 6 : 5. Ratio of eyes AME : ALE : PME : PLE = 13 : 8 : 10 : 8. AME separated from one another by about three-halves of their diameter, from ALE by nearly five-thirds of their diameter. PME separated from one another by slightly more than their diameter, from PLE by nearly four diameters. Laterals separated from one another by five-eighths of their diameter. Two long slender spines just posterior to LE and a row of four similar spines between ME. Height of clypeus equal to slightly more than the diameter of AME. Secondary sexual characters on maxillae, first coxae, and second femur as usual.

Legs. 1243. Width of first patella at "knee" .303 mm., tibial index of first leg 8. Width of fourth patella at "knee" .271 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.445	.910	2.730	2.340	.975	10.400
2.	2.470	.780	1.787	1.885	.910	7.832
3.	1.625	.585	.910	.942	.747	4.809
4.	2.405	.780	1.560	1.755	.780	7.280
Palp	.379	.271	.195	——	.780	1.625

Spines are largely removed from the hypotype through handling and long preservation. However, the following records are probably fairly accurate: the first femur appears to have two ventral spines on the promargin and one on the retromargin



External Anatomy of *Eustala*
Figures 63-68, *E. guttata*
Figures 69-72, *E. inconstans* sp. nov.

Fig. 63. Left second tibia of male from below.
Fig. 64. Right fourth femur of male from below.
Fig. 65. Left male palpal tarsus, lateral view.
Fig. 66. Uncus of the same, somewhat enlarged.
Fig. 67. Left male palpal tarsus from in front.
Fig. 68. Epigynum from below.
Fig. 69. Left tibia from below.
Fig. 70. Right fourth femur from below.
Fig. 71. Left male palpal tarsus, lateral view.
Fig. 72. Left male palpal tarsus from in front.

near the distal end; the second femur appears to have only one ventral spine on the promargin near distal end; ventral and related spines on the second tibia are shown in Figure 63; the third femur has a definite double series of ventral spines with three or four on each margin; the ventral spines of the fourth femur are shown in Figure 64.

Palp. Features of femur, patella, and tibia appear to be typical of the genus. Tarsus: the basal apophysis essentially as usual; clavis, somewhat damaged, but appears to be moderately robust with small articular surfaces at its base; the uncus is a pointed hook with a distinct shoulder at its base; the conductor is smaller proportionately than in many species and has a moderately setose shallow excavation on its distal surface together with two other more or less distinctive surfaces; the terminal laminae show a series of strongly chitinized ridges; the embolus is moderately long and slender (Figs. 65-67).

Female hypotype. Total length 5.525 mm. Body form like that of male.

Legs. 1243. Width of first patella at "knee" .379 mm., tibial index of first leg 10. Width of fourth patella at "knee" .357 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.575	1.202	2.795	2.260	.975	10.607
2.	2.990	1.170	2.307	1.950	.942	9.359
3.	1.755	.715	1.040	1.040	.682	5.232
4.	2.860	1.105	1.820	1.820	.780	8.385

First femur with a pair of ventral spines near distal end; the remaining femora apparently lacking the ventral spines.

Epigynum. Pattern of spermathecae, tubules, and apertures much as in *E. scutigera* and some other species; the most distinctive features appear to be the expanded auricular regions at base of scape on each side (Fig. 68).

Color in alcohol. The hypotype male is discolored from long preservation. The more recently collected males and females show a highly variable color pattern the more persistent features of which appear to be the following: a well developed dorsal folium which is itself highly variable in color; a transverse row of four small brownish dots across the carapace at about the

middle of the thoracic groove and a transverse row of two similar spots at the base of pars cephalica; with a ventral elongated whitish spot in the center of a dark area between the genital groove and spinnerets.

Type locality. Male hypotype from San Jose, Costa Rica (Tristan); probably collected a few years before 1909. Female hypotype from Barro Colorado Island, C. Z., July, 1950. In the various collections which I have had the opportunity of studying, I have seen what I consider to be this species from many localities in Mexico, Guatemala, Honduras, and Panama.

Eustala inconstans sp. nov.

(Figures 69-72)

Male holotype. Total length 4.485 mm. Carapace 2.210 mm. long; 1.852 mm. wide opposite interval between second and third coxae where it is widest; .910 mm. tall and, therefore, about .49 as tall as wide; gently inclined from PME to beginning of steep posterior declivity opposite interval between second and third coxae; with well developed median longitudinal thoracic groove; with spines confined to ocular area; apparently with a rather sparse covering of procumbent, light colored hair; without definite tufts of hair behind PLE but with a group of eight to ten bristles or spinules in this position.

Eyes. As usual, eight in two rows, all dark; LE on moderately prominent tubercles. Viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers. Central ocular quadrangle wider in front than behind in ratio of about 5 : 4; wider in front than long in ratio of nearly 9 : 8. Ratio of eyes AME : ALE : PME : PLE = 11 : 8 : 9.5 : 7.5. AME separated from one another by three-halves of their diameter, from ALE by nearly five-thirds of their diameter. PME separated from one another by slightly more than their diameter, from PLE by about seven halves of their diameter. Laterals separated from one another by three-fifths of the diameter of PLE. Height of clypeus equal to slightly more than the diameter of AME.

Chelicerae. Basal segment .55 mm. long; transversely rugulose on anterior surface. Fang groove well defined; promargin and

retromargin appear to have the usual complement of teeth but inspection is impossible without serious injury to holotype. Otherwise typical of the genus in all observed features.

Maxillae. Apparently as usual in all observed features including the maxillary tooth used in opposition to the femoral palpal ridge.

Lip. Wider than long in ratio of about 3 : 2; cross striated in basal half. Sternal suture definitely procurved.

Sternum. Scutiform; longer than wide in ratio of 11 : 8; not definitely continued between fourth coxae which are separated by about one-fifth of their width; with the usual supply of long stiff bristles or spinules.

Legs. 1243. Width of first patella at "knee" .314 mm., tibial index of first leg 9. Width of fourth patella at "knee" .271 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.925	1.072	2.340	2.210	.942	9.489
2.	2.405	.942	1.755	1.885	.780	7.767
3.	1.495	.520	.747	.780	.552	4.094
4.	1.900	.877	1.300	1.667	.760	6.504
Palp	.347	.227	.162	——	.942	1.678

Ventral hook on first coxa typical of the genus; dorsal tubercle on first coxa poorly indicated; prolateral basal ridge and groove on second femur well developed.

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral the same with the first two long and robust, retrolateral 0-0-0-0-1-1, ventral promargin 0-0-1-0-1, retromargin 0-0-0-1-1; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-0-1-1-0, prolateral and retrolateral 0-1-0-1-1, ventral 2-lp-2 (irregular)-0-2; metatarsus dorsal 0-1-0-1-0, prolateral 0, retrolateral 0-1-0-1-0, ventral 2-2(irregular)-lp-0. Second leg: femur dorsal and retrolateral as in first, prolateral 0-0-0-1-1, ventral promargin only one near distal end and retromargin 0-0-1-0-0; patella as in first; tibia dorsal 0-1-0-1-1-0, prolateral 0-1-1-1, retrolateral 0-1-1-0, ventral 2-lp-lp-lp-2 (Fig. 69); metatarsus dorsal 0-1-0-0-0, prolateral 0-1-0, retrolateral 0-1-0-0, ventral

lr-lp-lr-lp-lr-0. Third leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral 0; patella 1(weak)-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-0-1-0, prolateral and retrolateral 0-1-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral and retrolateral 0-1-0, ventral lp-lp-lp. Fourth leg: femur as in third except ventral as shown in Figure 70; patella as in third; tibia dorsal 0-1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-1, ventral 2-lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-1-0-1-0, ventral 0-lp-0-1.

Palp. Complicated; basal femoral ridge, patella, and tibia essentially typical of the genus. Tarsus: basal apophysis a distorted arrow-head shape distally as usual; the clavis is moderately robust and somewhat excavated at its base; the uncus is of moderate length and a robust and twisted hook; the conductor is relatively small, moderately concave on its anterior surface where it is finely setose; the vesicle is apparently withdrawn to the interior and is nearly invisible externally; the embolus is short and appears sharply pointed when viewed in the ordinary way, and is very distinctive in appearance; the terminal laminae are massive, with a large tubercle close to the base of the clavis (Figs. 71-72).

Abdomen. Total length 2.470 mm.; 1.852 mm. wide about one-fourth from base; with the usual round-triangular form; with the usual supply of long, slender, dorsal, and dorsolateral spinules. Other observed features typical of the genus.

Color in alcohol. Carapace unicolorous yellowish except for faint dots as they occur in so many species of the genus; probably here in two rows of two and four as described in *E. guttata.* The sternum is a pale yellow throughout. The legs are yellowish with faint indications of the usual brown bars, rings, and spots which would show more or less clearly in many other members of the species. Abdomen: the dorsal folium barely indicated; general color of dorsum and lateral sides whitish from the presence of many subchitinous white granules; the venter is yellowish white without distinctive markings.

Type locality. The holotype is from Barro Colorado Island, C. Z., June, 1950. There are no paratypes.

Eustala ingenua sp. nov.

(Figure 73)

Female holotype. Total length 4.745 mm. Carapace 2.080 mm. long; 1.885 mm. wide opposite second coxae where it is widest; .780 mm. tall and, therefore, about .41 as tall as wide; median thoracic groove well defined; with what appears to be only a sparse coat of light colored procumbent hair.

Eyes. Eight in two rows, all dark; viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 28 : 25, slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 8 : 6.5 : 8 : 6.5. AME separated from one another by seven-fourths of their diameter, from ALE by nearly three times their diameter. PME separated from one another by nearly 1.5 times their diameter, from PLE by four times their diameter. Laterals separated from one another by ten-thirteenths of their diameter. Height of clypeus equal to about three-fourths of the diameter of AME.

Chelicerae. Basal segment .675 mm. long; general features typical of the genus. Fang groove with four promarginal and three retromarginal teeth as usual.

Maxillae. Appear to be completely typical of the genus in all observed features.

Lip. Wider than long in ratio of about 4 : 3; reaches slightly beyond the middle of the maxillae. Sternal suture distinctly procurved and with anterolateral angles of sternum produced into distinct tubercles.

Sternum. Scutiform; longer than wide in ratio of 8 : 7; bluntly pointed at posterior end which is not continued between fourth coxae which are separated by about one-sixth of their width; with low convexities opposite all coxae; with the usual stiff bristles (spinules).

Legs. 1243. Width of first patella at "knee" .3141 mm., tibial index of first leg 11. Width of fourth patella at "knee" .2708 mm., tibial index of fourth leg 13.

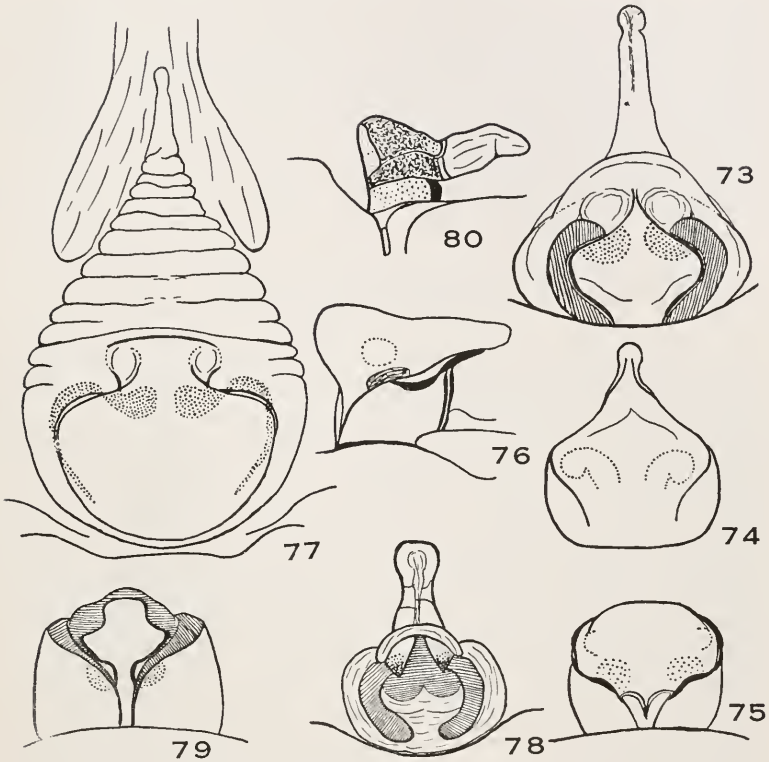
	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.470	1.040	1.936	1.760	.758	7.964
2.	2.275	.990	1.755	1.625	.747	7.392
3.	1.365	.575	.704	.747	.520	3.911
4.	2.080	.836	1.325	1.495	.585	6.321

Spines. First leg: femur dorsal 0-0-1-0-1, prolateral 0-0-1-1-1 (first two long and robust), retrolateral 0-0-0-0-1-1, ventral only one near distal end on both promargin and retromargin; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1; tibia dorsal 1-1-1-0, prolateral and retrolateral 0-1-1-1, ventral 2-lp-2-0-2; metatarsus dorsal 0-1-1-0-0, prolateral 0; retrolateral 0-1-1-0, ventral lr-2-lp-0 on left and 2-2-lp-0 on right. Second leg: femur as in first except that the two corresponding to the two large prolaterals are small; patella as in first; tibia essentially as in first; metatarsus as in first except ventral lr-lp-lr-lp-0-0. Third leg: femur dorsal 0-1-1-0-1, prolateral and retrolateral only one near distal end, ventral 0 but several spinules suggest normal spines; patella probably only dorsal 1-1; tibia dorsal 1-0, prolateral 0, retrolateral 0-1, ventral lp-lp-2; metatarsus dorsal 0-1-1-0-0, prolateral 0-1-0-0, retrolateral 0, ventral lp-lp-1-1. Fourth leg: femur as in first except ventral one on retromargin near distal end; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-1; tibia dorsal 1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-0-1, ventral lp-lp-lp-2; metatarsus dorsal 0-1-1-0-0, prolateral 0-1-1-1, retrolateral 0-1-1-0, ventral 0-lp-lp-0-1.

Abdomen. 3.25 mm. long; 2.73 mm. wide about one-fourth from base where it is widest; with numerous long slender spines; other features essentially typical of the genus.

Epigynum. Quite distinctive; with a relatively long and slender scape which arises abruptly from the base which is considerably wider than long; the apertures are separated by less than the diameter of one of them (Fig. 73). The base is not extended; hence it seems unnecessary to include a figure drawn from the lateral aspect.

Color in alcohol. Both of the available specimens of this species agree well in coloration. Carapace yellowish with poorly defined light reddish brown streaks passing from anterior end of the thoracic groove to the ocular region. Sternum yellowish. Legs:



External Anatomy of *Eustala*
Figure 73, *E. ingenua* sp. nov.
Figures 74-76, *E. innoxia* sp. nov.
Figure 77, *E. lata* sp. nov.
Figures 78-80, *E. latebricola*

Fig. 73. Epigynum from below.
Fig. 74. Epigynum from below.
Fig. 75. Epigynum, a more posterior view.
Fig. 76. Epigynum, lateral view.
Fig. 77. Epigynum from below.
Fig. 78. Epigynum from below.
Fig. 79. Epigynum, a more posterior view.
Fig. 80. Epigynum, a lateral view.

different shades of amber yellow. Abdomen: dorsal and dorsolateral regions yellowish white from many subchitinous granules; venter yellowish and also with many subchitinous whitish granules; just posterior to the genital groove there is a poorly defined elongated whitish spot.

Type locality. Holotype and one paratype female are from Summit, C. Z., July, 1950.

Eustala innoxia sp. nov.

(Figures 74-76)

Female holotype. Total length 5.135 mm. Carapace 2.015 mm. long; 1.592 mm. wide opposite interval between second and third coxae where it is widest; .780 mm. tall and, therefore, about .49 as tall as wide; median longitudinal thoracic groove well defined but apparently not as pronounced as in the more typical members of the genus; with a moderately well developed coat of yellowish hair raised into a rather poorly developed tuft accompanied by bristles just posterior to PLE; with two long slender spinules centrally placed behind PME and further behind these a short distance anterior to the thoracic groove are probably six similar spines in two rows of three each.

Eyes. Eight in two rows, all dark as usual; viewed from above, posterior row moderately recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of about 11 : 10, as long as wide in front. Ratio of eyes AME : ALE : PME : PLE = 11 : 9 : 10 : 7.5. AME separated from one another by their diameter, from ALE by about four-thirds of their diameter. PME separated from one another by nine-tenths of their diameter, from PLE by slightly less than three times their diameter. Laterals separated from one another by two-thirds of the diameter of PLE. Height of clypeus equal to seven-elevenths of the diameter of AME.

Chelicerae. Basal segment .780 mm. long; fang groove well developed and with four retromarginal and three promarginal teeth as usual. Other observed features typical of the genus.

Maxillae. Appear to be completely typical of the genus in all observed features.

Lip. Wider than long in ratio of nearly 4 : 3; gently grooved and cross striated in basal third. Sternal suture distinctly procurved; with no marked anterolateral sternal tubercles at ends of the suture.

Sternum. Scutiform; only slightly longer than wide; not continued between fourth coxae which are separated by about one-fifth of their width; with only slight convexities opposite each coxa; probably in life with the usual supply of long stiff bristles (spinules).

Legs. 1243. Width of first patella at "knee" .2816 mm., tibial index of first leg 8. Width of fourth patella at "knee" .2599 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.315	1.007	2.665	2.405	1.040	10.432
2.	2.600	.900	1.950	1.950	.910	8.310
3.	1.540	.572	.836	.996	.650	4.594
4.	2.535	.836	1.386	1.694	.770	7.221

Spines. First leg: femur dorsal 0-1-1-0-0-1, prolateral 0-0-1-1-1-1, retrolateral only one near distal end, ventral probably none but some might regard spinules present as weak spines and worth recording; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 1-1; tibia dorsal 0-1-0-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-1-1-0, ventral lp-0-lr-lp-0-lr; metatarsus dorsal 0-1-1-0-0, prolateral 0, retrolateral 0-1-1-0, ventral 0-lr-0-0. Second leg: femur dorsal as in first, prolateral and retrolateral only one near distal end, ventral 0; patella dorsal as in first, prolateral 0, retrolateral as in first on right but on left 0-1; tibia dorsal and retrolateral as in first, prolateral 0-1-0-1-0, ventral (only bristle)-2-lr; metatarsus dorsal 0-1-1-0, prolateral 0-1-0-0, retrolateral 0-1-1-0, ventral only bristles. Third leg: femur dorsal 0-1-0-0-1, prolateral and retrolateral only one near distal end, ventral only bristles or spinules; patella only dorsal 1-1; tibia dorsal 1-0-1-0, prolateral 0, retrolateral 0, ventral lp-lp-2; metatarsus dorsal 0-1-1-0-0, prolateral and retrolateral 0, ventral 0-lp-lp. Fourth leg: femur dorsal 0-1-0-1-1(last one duplicated on left), prolateral and retrolateral only one near distal end, ventral two on retromargin near distal end; patella dorsal and prolateral as in third, retrolateral 0-1; tibia dorsal

0-1-0-1, prolateral 0-1-1-1, retrolateral 0-0-1-1-1-1, ventral lr-0-lr; metatarsus dorsal 0-1-0-0, prolateral and retrolateral 0-1-0, ventral 0.

Abdomen. 3.120 mm. long; 3.445 mm. wide near middle; tall as well as broad and, therefore, not of the usual *Eustala* form; with numerous slender spines of moderate length; other features appear to be fairly typical of the genus.

Epigynum. Simple as compared to the typical organ in the genus; the scape is short and broadly attached to the base which is relatively massive; apertures hidden (Figs. 74-76).

Color in alcohol. Carapace: yellowish with a black dot on each side at base of pars cephalica and on a line with the LE; also with a few faint irregular grayish spots on the pars cephalica. Sternum: yellowish with faint grayish spots opposite the coxae. Legs: yellowish with a few grayish spots. Abdomen: the dorsal folium moderately well outlined in posterior half; most of the dorsal and dorsolateral areas are white from many subchitinous granules; there is also a narrow dark transverse wavy line just in front of the middle; the venter is generally yellowish with scattered white subchitinous granules; a few dark subchitinous spots occur irregularly in the anterior third of the venter; there is an incomplete dark ring around the spinnerets and an accumulation of white granules in the center behind the genital groove make a poorly outlined central white spot.

Type locality. The holotype and one female paratype are from the Canal Zone Forest Reserve, C. Z., August, 1939.

Eustala lata sp. nov.

(Figure 77)

This specimen had recently moulted when taken and is somewhat fragile but is in fair condition.

Female holotype. Total length 8.255 mm. Carapace 3.640 mm. long; 3.380 mm. wide opposite interval between second and third coxae where it is widest; 1.170 mm. tall and, therefore, about .35 as tall as wide; median longitudinal thoracic groove well defined as usual; with a well developed coat of yellowish procumbent hair and numerous brownish spinules over much of the surface and with tufts of the hair behind PLE.

Eyes. Eight in two rows, all dark as usual; viewed from above, posterior row rather strongly recurved; viewed from in front, anterior row definitely procurved; central ocular quadrangle wider in front than behind in ratio of 46 : 41, wider in front than long in about the same ratio. Ratio of eyes AME : ALE : PME : PLE = 11 : 9 : 10 : 10. AME separated from one another by nearly three diameters of one of them, from ALE by about four diameters of one of them. PME separated from one another by 2.5 times their diameter, from PLE by a little more than seven times their diameter. Laterals separated from one another by eleven-ninths of the diameter of ALE. Height of clypeus equal to a little less than twice the diameter of AME.

Chelicerae. Basal segment 1.365 mm. long; fang groove well developed; promargin with four teeth and only the last one is noticeably smaller; retromargin with four fairly robust teeth (one of the rare instances in the genus); other observed features appear to be typical of the genus.

Maxillae. Appear to be typical of the genus in all observed features.

Lip. Wider than long in ratio of 5 : 4; gently grooved and cross striated in basal third. Sternal suture distinctly procurved.

Sternum. Scutiform; longer than wide in ratio of about 3 : 2; anterolateral corners produced into distinct tubercles at ends of sternal suture; posterior end bifurcated and not continued between fourth coxae which are separated by about one-fifth of their width; with the usual supply of longer and shorter stiff spinules.

Legs. 1243. Width of first patella at "knee" .5848 mm., tibial index of first leg 10. Width of fourth patella at "knee" .5957 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.420	1.950	3.850	3.705	1.495	15.320
2.	4.030	1.950	3.250	3.510	1.495	14.235
3.	2.600	1.235	1.452	1.755	1.040	8.082
4.	3.850	1.885	2.860	3.120	1.250	12.965

Spines. First leg: femur dorsal 0-0-1-0-1, prolateral 0-0-1-1-0-1 on right and 0-0-1-1-1-0-1 on left, retrolateral 0-0-0-0-1-1, ventral three along promargin all in distal half and only one on retro-

margin near distal end but a row of spinules along retromargin suggests suppressed spines; patella dorsal 1-1, prolateral and retrolateral 1-1-0; tibia dorsal 0-1-1-1-0, prolateral 0-1-0-0-1, retrolateral 0-1-0-1-1, ventral 2-lp-2-0-2; metatarsus dorsal 0-1-1-0, prolateral 0-0-1-1, retrolateral 0-1-1-0, ventral 2-2-0-lr-0. Second leg: femur dorsal as in first, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1, ventral only one definite spine on retromargin near distal end but there is a row of eight or nine spinules before this: patella as in first; tibia dorsal as in first, prolateral and retrolateral 0-1-1-1, ventral 2-lp-2-lr-2; metatarsus dorsal 0-1-1-0, prolateral and retrolateral essentially like dorsal, ventral 2-lp-lr-lp-lr-lp. Third leg: femur dorsal 0-1-0-1-1, prolateral 0-0-0-1-1, retrolateral only one near distal end, ventral apparently 0; patella dorsal as in first, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 1-0-1-0, prolateral 0-0-1-1, retrolateral 0-0-1, ventral apparently lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0-1-1, retrolateral 0, ventral lp-lp-2-lp. Fourth leg: femur dorsal essentially as in third, prolateral and retrolateral only one near distal end, ventral only one on retromargin near distal end; patella as in third; tibia dorsal 1-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-1-1, ventral 2?-0-lp-lp-2; metatarsus dorsal 0-1-1-0, prolateral 0-1-1-1, retrolateral 0-1-1-0, ventral lp-lp-lp-lp. Tarsal claws as usual in the genus. Palpal claw pectinate in a single row of eight teeth; the distal two robust, others very slender.

Abdomen. 5.01 mm. long; 4.420 mm. wide about one-third from base; with the usual round-triangular form; with many slender spines of moderate length; without the long spines which often occur in *Eustala;* other features appear to be typical of the genus, except that two small posterior tubercles suggest a potential bifid condition.

Epigynum. Nearly twice as long as wide at base of scape; scape gradually narrowed to tip; tubules form an oval area at base; apertures small and nearly two diameters apart; unextended so as to be only partly visible in profile (Fig. 77).

Color in alcohol. Holotype recently moulted and normal color probably not well established. Cephalothorax, legs, and mouth parts light yellowish; four small dark spots faintly outlining a square in middle of dorsal area; legs with indications of large dark spots on many segments. Abdomen: dorsum whitish with

small reddish dots and a mixture of grayish and greenish streaks; with a fairly well defined folium; venter with a large black median spot enclosing a white spot of irregular shape.

Type locality. Holotype from Barro Colorado Island, C. Z., August, 1950. No paratypes have appeared in my collection.

Eustala latebricola (O. P. Cambridge), 1889

(Figures 78-80)

Epeira latebricola O. P. Cambridge, 1889
E. latebricola Keyserling, 1892
Eustala latebricola F. P. Cambridge, 1904
E. bifida Banks, 1909 (in part)
E. latebricola Petrunkevitch, 1911
E. latebricola Petrunkevitch, 1925

Female hypotype. Total length 4.875 mm. With the body form ordinarily described as round-triangular; with what appears to be nearly suppressed shoulder humps. The central ocular quadrangle as wide behind as in front; wider than long in ratio of 10 : 9. Ratio of eyes AME : ALE : PME : PLE = 9 : 8 : 9 : 7. AME separated from one another by five-thirds of their diameter, from ALE by eight-thirds of their diameter. PME separated from one another by about 1.5 of their diameter, from PLE by about four times their diameter. Laterals separated by three-fourths of the diameter of ALE. Height of clypeus slightly greater than the diameter of AME. Promargin of fang groove with four teeth, the second and fourth smaller; retromargin with three teeth.

Legs. 1243. Width of first patella at "knee" .3249 mm., tibial index of first leg 9. Width of fourth patella at "knee" .325 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.990	1.105	2.405	1.950	.975	9.425
2.	2.470	1.040	1.950	1.755	.845	8.060
3.	1.527	.617	.758	.812	.585	4.299
4.	2.405	.975	1.430	1.462	.715	6.987

The hypotype seems to lack ventral femoral spines but some specimens have a pair of ventral spines on the first and last

femora near the distal end.

Epigynum. Quite distinctive; the scape is bluntly rounded at the distal end and somewhat constricted in the middle; there is a groove and a ridge, semicircular in shape, at the base of the scape; the base itself is very prominent in the middle as seen in posterior view (Figs. 78-80).

Color in alcohol. The general color pattern is, as usual, exceedingly variable; the folium is often well developed but it may be almost completely lacking; the transverse row of four small dots across the carapace at the level of the posterior third of the thoracic groove and the transverse row of two dots at the base of the pars cephalica are present in the hypotype but are sometimes reduced in number or lacking altogether; the elongated white spot in the center of a dark area on the venter is usually present.

Type locality. The Cambridges had this species from Guatemala and Panama. The hypotype is from Boquete, R. P., August, 1950. In addition to the single female sent from the British Museum I have several females from Boquete, R. P., July, 1939 and August, 1950. Numerous specimens labelled *E. bifida* Cb. and, presumably, reported by Banks (1909) as *E. bifida* are in reality *E. latebricola* (O. P. Cambridge).

Eustala longembola sp. nov.

(Figures 81-85)

Male holotype. Total length 4.29 mm. Carapace 2.210 mm. long, 1.885 mm. wide between intervals separating second and third coxae where it is widest; .845 mm. tall and, therefore, about .45 as tall as wide; rises gradually from PME to opposite interval between second and third coxae from where it descends to posterior margin; with a well developed longitudinal thoracic groove; with a few weak spines and a sparse coating of procumbent brown hair.

Eyes. Eight in two rows, all dark; LE on moderately prominent tubercles; viewed from above both rows of eyes strongly recurved; viewed from in front, anterior row somewhat procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 35 : 28; wider in front than long in ratio of 35 : 32. Ratio of eyes AME : ALE : PME : PLE =

11 : 7 : 9 : 7. AME separated from one another by about fourteen-elevenths of their diameter, from ALE by eighteen-elevenths of their diameter. PME separated from one another by four-thirds of their diameter, from PLE by nearly five times their diameter. Laterals separated from one another by four-sevenths of their diameter. Clypeus very receding. Height of clypeus equal to slightly more than the diameter of AME.

Chelicerae. Essentially parallel, but distal half is somewhat excurved; with moderately well developed basal boss; basal segment .617 mm. long, and somewhat cross striated in front. Fang groove well defined; promargin with four teeth, fourth somewhat isolated from others; retromargin with three teeth of moderate size. Fang evenly curved as usual.

Maxillae. In general as in male of *E. mexicana* in all observed features.

Lip. Wider than long in ratio of about 7 : 5; extends only a little beyond middle of maxillae; basal half somewhat cross striated. Sternal suture moderately procurved.

Sternum. Scutiform; longer than wide in ratio of 19 : 16; a sclerite continues from posterior end between fourth coxae which are almost in contact; covered with long curved bristles.

Legs. 1243. Width of first patella at "knee" .3249 mm., tibial index of first leg 8. Width of fourth patella at "knee" .2708 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.445	1.137	2.730	2.210	.910	10.432
2.	2.600	.942	1.820	1.885	.910	8.157
3.	1.495	.585	.845	.845	.585	4.355
4.	2.210	.910	1.560	1.625	.715	7.020
Palp	.412	.217	.162	——	.780	1.571

First coxa with a well developed ventral distal retromarginal hook; prolateral groove at base of second femur also well developed; dorsal tubercle on first coxa moderately well developed.

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral and retrolateral the same, ventral apparently 0-lp-0-0-2 (considerable variation has been noted among paratypes); patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-0-1-0; tibia dorsal 0-1-0-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-2-2-lp-2 with some

irregularities between right and left; metatarsus dorsal 0-1-1-0, prolateral 0-1-0-1-0, retrolateral 0-1-1-0, ventral lr-lr-0-0. Second leg: femur as in first except ventral spines apparently consist of only a pair near distal end; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1-0; tibia dorsal 0-1-1-1-0; prolateral and retrolateral 0-1-1-0, ventral 2-lp-2-lp-2 (Fig. 81); metatarsus dorsal 0-1-0, prolateral 0, retrolateral 0-1-1-0, ventral lr-lp-lr-lp-0. Third leg: femur dorsal 0-1-1-1, prolateral and retrolateral 0-0-1, ventral 0-lp-lp-0; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-0-1-0; tibia dorsal 0-1-0-1-0, prolateral 0-1-0, retrolateral 0-1-1, ventral 0-lr-lr-lr; metatarsus dorsal 0-1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral lr-lr-lr. Fourth leg: femur essentially as in third except ventral with nine on right as in Figure 82 or six on left; patella essentially as in third; tibia dorsal 0-1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-1, ventral 2-lp-lp-2; metatarsus dorsal 0-1-0-1-0, prolateral 0-1-1-0, retrolateral 0-0-1-1-0, ventral 0-lp-0-lp.

Palp. Complicated; basal femoral tubercle or ridge opposing the maxillary tooth well developed; the patella is short, with a weak basal dorsal spine and a long slender distal dorsal spine; the patella also has a well developed distal retrolateral tubercle which is assumed to act in opposition to one of the other nearby chitinized structures; the tibia has the characteristic tri-lobed structure with each lobe well developed. Tarsus: the basal tarsal apophysis only slightly distorted from an arrow-shape; the clavis is rather slender, not excavated basally; the uncus is sharply pointed with a well developed shoulder at its base; the conductor is relatively simple, with an excavation on its distal face; the vesicle is large, nearly as extensive as the embolus; the embolus is long, slender, and curves along the whole distal border; the terminal laminae are only moderately grooved but they are provided with a series of thin strongly chitinized raised surfaces (Figs. 83-85).

Abdomen. Total length 2.405 mm.; rounded at both ends, with obscure triangular form; longer than wide in ratio of 37 : 27; with the usual long slender dorsolateral and dorsal spines; with other features as usual in the genus.

Color in alcohol. Carapace yellowish with a brownish dot on each side near posterior end of the thoracic groove and another

similar dot on each side near the anterior end of the groove; there are indications also of more or less extensive irregular brownish spots including much of the anterior half; these latter markings are conspicuous in some paratypes but lacking in others; the dots appear to be quite consistent in the paratypes. Sternum: yellowish with only faint blotches of gray around the margin. Mouth parts mostly yellowish but brownish flecks may occur. Legs: with many brownish rings, bars, and spots. Abdomen: dorsal folium narrow in front, with a narrow brown margin around posterior two-thirds; venter with a somewhat irregular quadrilateral spot between genital groove and base of spinnerets bearing a small central white spot. These ventral markings show variations among paratypes but seem to be fundamentally quite persistent.

Type locality. Holotype male from Barro Colorado Island, C. Z., August, 1939. Male paratypes from the following localities: Barro Colorado Island, C. Z., June-July, 1934; June-August, 1936; July-August, 1939; June-August, 1950; Arraijan, R. P., August, 1950; C. Z. Forest Reserve, C. Z., August, 1936 and July-August, 1939; Ft. Sherman, C. Z., August, 1939; El Valle, R. P., July, 1936; Madden Dam Forest, C. Z., August, 1939 and July, 1950; C. Z. Experiment Station, Summit, C. Z., July-August, 1950; near Chiva, C. Z., August, 1950; Chilibre, C. Z., July, 1950; Variedades, Guatemala, August, 1947 (C. and P. Vaurie).

Eustala maxima sp. nov.

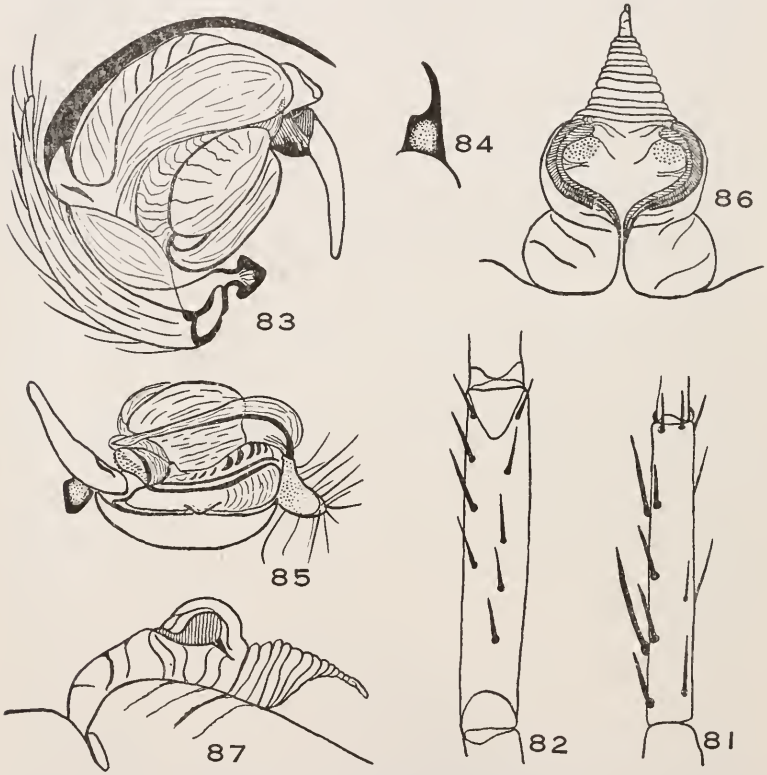
(Figures 86-87)

This is the species which has been repeatedly identified as *E. bifida* F. P. Cambridge. I am now convinced that it is distinct from the latter and inclined to believe that it is the female of *M. banksi* sp. nov. but there can be no certainty at present.

Female holotype. With the usual round-triangular form; total length 10.34 mm. Carapace 3.64 mm. long; 3.12 mm. wide opposite interval between second and third coxae where it is widest; 1.30 mm. tall and, therefore, about .42 as tall as wide; with median longitudinal thoracic groove well developed; with few if any spines except in ocular region; with a well developed coat

of almost white procumbent hair.

Eyes. Eight in two rows as usual, all dark; viewed from above, both rows strongly recurved; viewed from in front, anterior row moderately procurved, measured by centers; central ocular



External Anatomy of *Eustala*
Figures 81-85, *E. longembola*
Figures 86-87, *E. maxima*

Fig. 81. Left second tibia from below.
Fig. 82. Right fourth femur from below.
Fig. 83. Tarsus of male palp, lateral view.
Fig. 84. Uncus of the same somewhat enlarged.
Fig. 85. Tarsus of male palp, from distal end.
Fig. 86. Epigynum, from below.
Fig. 87. Epigynum, lateral view.

quadrangle exactly as wide in front as behind, slightly longer than wide. Ratio of eyes AME : ALE : PME : PLE = 12 : 9 : 13 : 10. AME separated from one another by slightly less than twice their diameter, from ALE by slightly more than four times their diameter. PME separated from one another by about 1.5 times their diameter, from PLE by nearly 5.5 times their diameter. Laterals separated from one another by a little more than two-thirds of the diameter of ALE. Height of the clypeus equal to the diameter of AME. A transverse row of four spinules extends between the rows of ME midway. Ventral border of clypeus with the usual row of stiff bristles.

Chelicerae. Moderately robust; essentially parallel; front surface with many slender spines. Basal segment 1.43 mm. long; with moderately well developed basal boss. Promargin of fang groove with four teeth, the fourth the smallest; retromargin with four teeth, all close together, the second the smallest; the fang is fairly robust, evenly curved, finely dentate along inner margin; the fang groove is well defined and finely dentate.

Maxillae. With all usual features well developed. There appears to be a somewhat suppressed maxillary tooth corresponding to the strongly chitinized tooth on all males.

Lip. Wider than long in ratio of about 31 : 24; transversely striated in basal two-fifths; bluntly pointed distally; reaches only slightly beyond middle of maxillae. Sternal suture distinctly procurved with distal lateral corners of the sternum extended forward.

Sternum. Scutiform; longer than wide in ratio of 3 : 2; continued between fourth coxae by a slender sclerite; with fourth coxae separated from one another by a little more than one-fourth of their width; with slight convexities opposite first, second, and third coxae.

Legs. 1243. Width of first patella at "knee" .5957 mm., tibial index of first leg 11. Width of fourth patella at "knee" .6065 mm., tibial index of fourth leg 14.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.640	1.950	3.380	3.380	1.397	13.747
2.	3.445	1.820	2.990	3.120	1.300	12.675
3.	2.340	1.105	1.300	1.625	.975	7.345
4.	3.380	1.690	2.535	2.860	1.170	11.635

Spines. First leg: femur dorsal 0-1-0-1-1, prolateral and retrolateral the same, ventral spines weak but probably with three or four on each margin and all in distal half; patella dorsal 1-1, prolateral and retrolateral 0-1-1-0; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-0-1-1(weak), ventral 2-lp-lr-lp-0-2; metatarsus dorsal 0-1-0-1-0, prolateral 0-1-1-0, retrolateral 0-0-1-0-1-0, ventral 2-2-2-0 with some irregularity. Second leg: essentially the same as the first with few exceptions. Third leg: femur essentially as in first and second; patella dorsal 0-1-0-1, prolateral 0-1-0, retrolateral 0; tibia dorsal 1-0-1-0, prolateral 1-1-1(first and last weak), retrolateral 0, ventral lp-lp-2; metatarsus dorsal 1-0-1-0, prolateral 1-0-1-0(both weak), retrolateral 0, ventral lp-lp-lp-2. Fourth leg: with few exceptions like third but differences seem unimportant. Palpal spines: femur dorsal 0-1-0-1; patella dorsal 1-1; tibia with several spines and numerous spinules; tarsus also with numerous spines and spinules. Palpal claw: pectinate in a single row of six or seven slender teeth. Tarsal claws three; proclaw with five or six teeth, retroclaw with eight slender teeth.

Abdomen. 6.50 mm. long; as wide as long; low convexities suggest suppressed shoulder humps; the posterior end is quite distinctly bifid dorsoventrally much like that of *E. bifida.* Otherwise essentially typical of the genus.

Epigynum. Bears a close resemblance to that of *E. bifida* F. P. Cambridge but there are clearly defined differences best shown in figures (Figs. 86-87).

Color in alcohol. Carapace yellowish, flecked with brown; with signs of dots and stripes as described for the male of *E. banksi* sp. nov. Legs yellowish with brown spots and broad irregular rings. Sternum yellowish with many subchitinous granules and a brownish margin. Abdomen: with a poorly defined dorsal folium; dorsum nearly white from the presence of many subchitinous yellowish-white granules; the venter has a somewhat quadrilateral dark area between the genital groove and the base of the spinnerets; a central elongated white granular spot extends through anterior half of the dark area.

Type locality. Holotype female from Summit, C. Z., July, 1950. Female paratypes from Barro Colorado Island, C. Z., July (Dodge); also from the Rau collection with no date.

Eustala mexicana sp. nov.
(Figures 88-89)

Female holotype. With the conventional round-triangular form; total length 5.20 mm. Carapace 2.08 mm. long, 1.80 mm. wide opposite interval between second and third coxae where it is widest; .65 mm. tall and, therefore, about .36 as tall as wide; with a well developed longitudinal thoracic groove; with a pair of slender spines at anterior end of thoracic groove and several other similar spines on cephalic part; also with a moderately well developed coat of light yellowish procumbent hair.

Eyes. Eight in two rows as usual, all dark; none particularly prominent; viewed from above both rows strongly recurved; viewed from in front, anterior row moderately procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 15 : 13, wider in front than long in ratio of about 15 : 13. Ratio of eyes AME : ALE : PME : PLE = 9 : 7 : 8.75 : 6.5. AME separated from one another by a little less than two diameters, from ALE by a little less than three diameters of AME. PME separated from one another by nearly one and one-third of their diameter, from PLE by four diameters of PME. Laterals separated by slightly more than one-half the diameter of ALE. Height of clypeus equal to about two-thirds of the diameter of AME. Ventral border of clypeus with a row of stiff bristles.

Chelicerae. Moderately robust, parallel; medially the anterior surface with numerous converging spine-like bristles. Basal segment .78 mm. long; with well developed basal boss. Promargin of fang groove with four teeth, second and fourth small, others moderately robust; retromargin with three moderately robust teeth, all in basal half. Fang moderately robust and evenly curved.

Maxillae. Essentially parallel; robust; with well developed scopula along medial border and inner distal corner; with well developed serrula along outer distal corner and adjacent distal and lateral surfaces.

Lip. Wider than long in ratio of about 4 : 3; broad distal border very full and well rounded; transversely excavated in basal two-thirds; reaches only slightly beyond middle of maxillae. Sternal suture distinctly procurved.

Sternum. Scutiform; only slightly longer than wide; slightly the widest between second coxae; not extended between fourth coxae which are separated by about one-fourth of their width; with moderately developed prominences opposite coxae.

Legs. 1243. Width of first patella at "knee" .3249 mm., tibial index of first leg 10. Width of second patella at "knee" .3141 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.055	1.040	2.340	1.690	.715	8.840
2.	2.405	.970	1.755	1.495	.747	7.372
3.	1.365	.650	.780	.715	.552	4.062
4.	2.275	.970	1.462	1.300	.650	6.657

Spines. First leg: femur dorsal 0-1-0-1-1, prolateral 0-1-1-1-0, retrolateral 0-0-0-1-1, ventral 0-0-1-0-1 on prolateral margin and one near distal end on retromargin; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-0-1-1(weak), ventral 2-lp-2-lp; metatarsus dorsal 0-1-0-1-0-0, prolateral apparently 0, retrolateral 0-1-0-1-0, ventral lr-2-lp-0. Second leg: femur dorsal and retrolateral as in first, prolateral 0-0-0-1-1-1(weak), ventral apparently only one weak spine near distal end on retromargin; patella as in first; tibia as in first except ventral lr-2-lp-lr-0; otherwise essentially as in first. Third leg: femur dorsal 0-1-0-1, prolateral and retrolateral apparently only one definite spine on each at distal end, ventral 0; patella only dorsal 1-1, and prolateral 0-1-0; tibia dorsal lr-lp, prolateral 0, retrolateral only one weak distal spine, ventral lp-lp-2; metatarsus dorsal lp-lr, prolateral 0-1-0, retrolateral apparently 0, ventral lp-lp-lp-lp (all weak and little more than bristles). Fourth leg: femur dorsal 0-1-0-1-1, ventral only one distal on retrolateral margin; patella retrolateral 0-0-1-0, elsewhere as in third; tibia dorsal 1-1-1, prolateral 1-1-0-1-1, retrolateral 0-1-1, ventral lp-lp-lp-lp-lp; metatarsus dorsal 1-1-0, prolateral 1-1-1, retrolateral 0-0-1(weak), ventral 0-1-1-1. Palpal spines: femur dorsal 0-1; patella dorsal 1-1, prolateral 0-1; tibia dorsal 0-1-0, prolateral 1-1, retrolateral 0-1 (weak), ventral 0; tarsus with numerous spines irregularly placed. Palpal claws: pectinate in a single row of about six or seven light colored teeth and difficult to distinguish clearly. Three tarsal claws as usual in the genus.

Abdomen. Round-triangular, viewed dorsally; shoulder humps barely distinguishable; with a slightly developed tubercle at posterior end; longer than wide between suppressed shoulder humps in ratio of about 7 : 6; with numerous moderately long slender spines. Otherwise as usual in the genus.

Epigynum. With a broad base and slender scape; difficult to describe but quite distinctive; apertures about two diameters apart (Figs. 88-89).

Color in alcohol. Carapace: light yellowish with poorly defined brownish radiations from the thoracic groove; dark pigment surrounds the eyes. Sternum: with a fairly broad brownish margin; yellowish elsewhere. Mouth parts yellowish, streaked with gray. Legs and palps yellowish with brownish bands. Abdomen: dorsal folium well marked, highly variegated; dorsolaterally are four yellowish spots on each side; the venter has a large median quadrilateral brownish spot between the genital groove and base of spinnerets; the brownish spot is nearly divided by a narrow white stripe and is bounded laterally on each side by a narrow, somewhat incurved stripe.

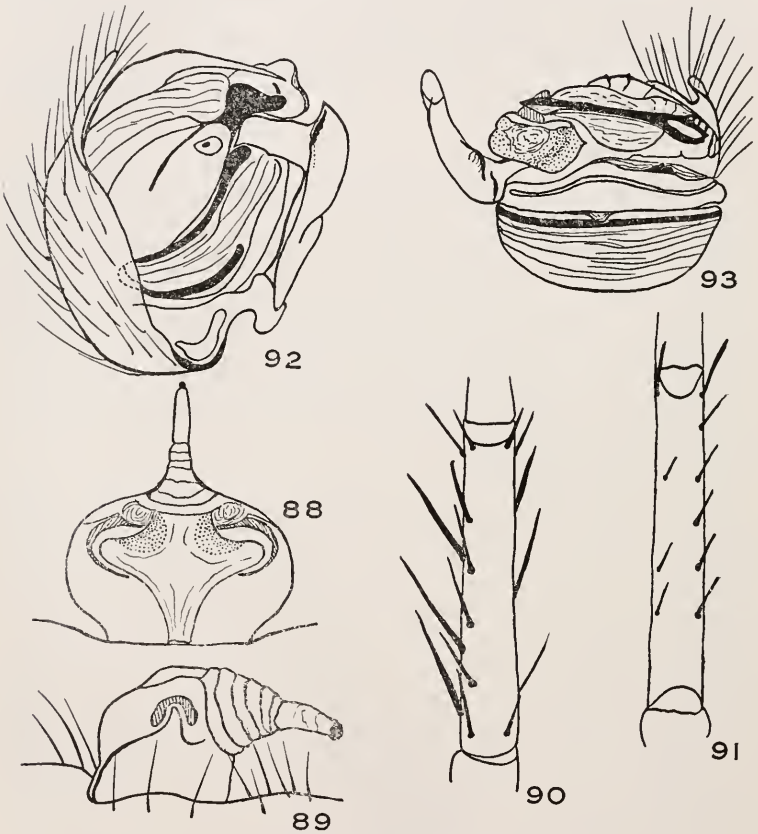
Type locality. Holotype female from Lo Bajo, Guerrera, Mexico, June, 1941 (L. I. Davis). Female paratypes from the following localities in Mexico: Boca de Pasquales, Colima, January, 1943 (F. Bonet); Chiapas, Rio de los Flores, near Cintalpa, September, 1947; Conjumatlan, Michoacan, June, 1941 (A. M. Davis); Hidalgo, Ixmiquilpan, August, 1947 (H. Wagner); Huajuapan, Oaxaca, Sept.-Oct., 1946 (H. Wagner); Nayerit, San Blas, August, 1947 (C. and M. Goodnight); Oaxaca, Tehuantepec, January, 1948 (T. MacDougal); Nayerit, Tepic, Sept., 1947 (B. Malkin); Teotitlan, Oaxaca, Sept., 1944 (H. Wagner); Tamaulipas, Santa Gracia, July, 1940 (Rau); Vera Cruz, Vera Crux, July, 1946 (H. Wagner).

Eustala mimica sp. nov.

(Figures 90-93)

All three specimens available to me for this study are in rather poor condition. The one chosen for the holotype has an injured and detached abdomen but is otherwise in good condition.

Male holotype. Total length about 7.48 mm. Carapace 4.225 mm. long; 3.185 mm. wide opposite interval between second and third coxae where it is widest; 1.365 mm. tall and, therefore,



External Anatomy of *Eustala*
Figures 88-89, *E. mexicana*
Figures 90-93, *E. mimica*

Fig. 88. Epigynum from below.
Fig. 89. Epigynum, lateral view.
Fig. 90. Left second tibia from below.
Fig. 91. Left fourth femur from below.
Fig. 92. Tarsus of male palp, lateral view.
Fig. 93. Tarsus of male palp from distal end.

about .43 as tall as wide; rises gradually from PME to highest point opposite interval between second and third coxae from where it slopes rather abruptly to posterior border; well rounded along margin from posterior border to opposite anterior border of third coxae and then with little change to opposite anterior border of second coxae from where it narrows to a blunt point in region of AME; longitudinal thoracic groove well marked with considerable convexity on each side; with two long slender spinules midway between AME and PME and two similar spinules on each side above LE.

Eyes. Eight in two rows, all dark; ocular tubercle bearing LE moderately prominent; viewed from above, both rows strongly recurved; viewed from in front, anterior row moderately procurved; central ocular quadrangle wider in front than behind in ratio of 8 : 7, nearly as wide in front as long. Ratio of eyes AME : ALE : PME : PLE = 9 : 5 : 7 : 5. AME separated from one another by nearly their diameter, from ALE by about five-thirds of their diameter. PME separated from one another by nine-sevenths of their diameter, from PLE by about three and one-half times their diameter. Laterals separated from one another by three-fifths of their diameter. Height of clypeus equal to eleven-ninths of the diameter of AME.

Chelicerae. With basal boss moderately well developed; basal segment 1.11 mm. long; each with numerous long slender spinules in front medially directed and overlapping; fang groove well marked, with four promarginal teeth the most distal of which is merely a dentule and with three retromarginal teeth of moderate size.

Maxillae. Essentially parallel; with the usual robust lateral tubercle opposed to the basal femoral palpal tubercle; other features as usual in the genus.

Lip. Wider than long in ratio of about 5 : 4. Sternal suture obscure but apparently gently procurved.

Sternum. Narrowly scutiform; mildly convex; moderately scalloped opposite coxae; longer than wide in ratio of 14 : 11; slightly widest at interval between second and third coxae but nearly as wide at interval between first and second coxae; posterior end continued as a very slender sclerite between fourth coxae which are separated by about one-fifth of their width.

Legs. 1243. Width of first patella at "knee" .585 mm., tibial index of first leg 9. Width of fourth patella at "knee" .520 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.550	2.015	4.355	4.160	1.625	16.705
2.	4.030	1.625	3.120	3.965	1.527	14.269
3.	3.250	1.105	1.625	1.755	1.000	8.735
4.	3.575	1.900	3.120	3.575	1.350	13.520
Palp	.550	.440	.308	——	1.298	2.596

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral the same with slight irregularities, retrolateral 0-0-0-0-1-1, ventral apparently 0-0-0-0-lp-2; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1-0; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 1-1-0-1-1 with some irregularities, ventral 2-lr-lp-2-lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1-0-1, retrolateral 0-1-1-0, ventral 2-2-2-lp with some irregularity. Second leg: femur as in first except only a single ventral pair near distal end; patella as in first; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0-1-1 (long and robust), retrolateral 0-1-1-1-1, ventral 2-lp-lp-lp-lp-2 (Fig. 90); metatarsus dorsal 0-1-0-0-0, prolateral 0-0-1-0-1, retrolateral 0-1-1-0, ventral 2-2-2-lp. Third leg: femur dorsal 0-1-0-1-1, prolateral and retrolateral 0-0-0-1-1, ventral 0-1-2-lr-2-2 (with some irregularity); patella dorsal 1(weak)-1, prolateral 1-0, retrolateral 0-1; tibia dorsal 1-0-1-0, prolateral 1-1-1, retrolateral 0-1-1, ventral lp-2-2-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral 2-2-2-lp. Fourth leg: femur dorsal 0-1-0-1-1, prolateral and retrolateral only one near distal end, ventral 0-2-2-lr-2-lr-2 (with some irregularity and differences on right and left) (Fig 91); patella dorsal and retrolateral 0-1, prolateral 0-1-0; tibia dorsal 0-1-0-1-1-0, prolateral 1-1-1-1, retrolateral 1-1-1, ventral 2-2-2-2 (with some differences between right and left); metatarsus dorsal 0-1-1-0-0, prolateral 0-1-1-1, retrolateral 0-0-1-1-1, ventral 2-2-2-2. Tarsal claws apparently as usual in the genus. Trichobothria numerous and apparently widely distributed at least on tibiae and metatarsi.

Palp. Very complicated as usual in the genus. Maxillary tubercle, basal femoral tubercle, and probably trochanteral tubercle as usual in the genus. There is a single slender distal dorsal

spinule on the femur and a single long dorsal distal patellar spine. The patella is short, simple, strongly chitinized along its distal prolateral boarder; the tibia is very short but relatively broad with less well marked trilobate form than in many species and with the usual strongly chitinized ventral collar. Tarsus: basal apophysis a somewhat distorted arrow-shape; the clavis is robust, without basal excavation; the uncus is robust, with a relatively long robust shank and a marked shoulder at base of terminal hook; the conductor is comparatively simple on the ventral surface but is provided with several characteristic distal surfaces with no slender extensions; the vesicle is small, otherwise normal; the embolus is a slender, strongly chitinized tube terminating in a lance-like tip; the terminal laminae are simple with no strongly developed characteristic folds (Figs. 92-93).

Abdomen. Badly shrunken and so distorted as to make it undesirable to describe it. Apparently with the usual round-triangular form (shown clearly in paratypes); with many stiff spinules of the common kind.

Color in alcohol. Cephalothorax, legs, and mouth parts with various shades of yellowish without conspicuous markings. Holotype abdomen unsuitable for description. Paratype abdomens show a median dark stripe along cardiac region, a fairly well defined dorsal folium. many subchitinous whitish granules, a large ventral black area enclosing a white spot broadened in the middle.

Type locality. Male holotype from Summit, C. Z., December, 1946 (N. L. H. Krauss). Two male paratypes from the Phil Rau collection in the Museum of Comparative Zoology with no accompanying collection data but I think these were taken during the winter months on Barro Colorado Island, C. Z.

Eustala minima sp. nov.

(Figures 94-96)

This species has hitherto been regarded as *E. fragilis* (O. P. Cambridge) but is now regarded as a species new to science. Unfortunately, *E. fragilis* was not included among the specimens loaned from the British Museum and, hence, it has been difficult to reach a decision in respect to the status of the species. How-

ever, a drawing kindly sent by Dr. G. Owen Evans has aided me in the final decision.

Female holotype. Of conventional, non-elongated, round-triangular form; total length 5.33 mm. Carapace 2.02 mm. long; 1.69 mm. wide opposite interval between second and third coxae where it is widest; .78 mm. tall and, therefore, about .46 as tall as wide; posterior declivity more precipitous than usual in the genus; median thoracic groove moderately well developed but relatively shorter than usual in the genus; with a group of several weak spines at anterior end of thoracic groove; with a transverse row of four slender spinules between ME; also with a moderately well developed coat of light colored procumbent hair.

Eyes. Eight in two rows, all dark; viewed from above, both rows moderately recurved; viewed from in front, anterior row slightly procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 28 : 25; longer than wide in front in ratio of 15 : 14. Ratio of eyes AME : ALE : PME : PLE = 11 : 8 : 8 : 8. AME separated from one another by slightly more than their diameter, from ALE by 15/11 of their diameter. PME separated from one another by their diameter, from PLE by 27/8 of their diameter. Laterals separated from one another by their radius. Height of clypeus equal to the diameter of AME.

Chelicerae. Basal segment .7 mm. long; general features as usual in the genus. Fang groove well defined and finely dentate; promargin with four teeth, second and fourth small, others of moderate size; retromargin with three teeth, the third the largest.

Maxillae and *Lip.* Typical of the genus in all observed features. Sternal suture procurved.

Sternum. Scutiform; almost exactly as wide as long; with only slight convexities at posterior end and opposite first, second, and third coxae; not continued between fourth coxae which are separated by a little less than one fifth of their width.

Legs. 1243. Width of first patella at "knee" .2924 mm., tibial index of first leg 9. Width of fourth patella at "knee" .2708 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.795	.977	2.307	2.210	.910	9.199
2.	2.370	.845	1.885	1.820	.700	7.620
3.	1.495	.600	.812	.866	.541	4.314
4.	2.340	.910	1.430	1.657	.650	6.987

Spines. First leg: femur dorsal irregular, 0-1-1-0-0-1 on right, 0-1-1-1-1-0-0-0-1 on left, prolateral 0-0-1-1-1-1-0, retrolateral apparently only one near distal end, ventral apparently only one weak spine on retromargin near distal end; patella dorsal 1-1, prolateral 1-0, retrolateral 1-1-1 on right, 1-1 on left; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-1-1-1, ventral 0-lr-2-lp; metatarsus dorsal 0-1-0-0-0, prolateral 0-1-0, retrolateral 0-1-1-1-0, ventral 0-2-lr-0-0. Second leg: femur dorsal 0-1-1-0-0-1, prolateral and retrolateral apparently only one near distal end, ventral 0; patella dorsal 1 (weak)-1, prolateral 0-1 (weak)-0, retrolateral 0-1; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-1-1, ventral 0-lr-2; metatarsus dorsal 0-1-1-0-0, prolateral apparently 0 but with several spinules, retrolateral 0-1-1-0, ventral 0-2-0-0. Third leg: femur dorsal 1-1(weak)-1, retrolateral apparently only one near distal end; patella apparently only dorsal 1-1, tibia dorsal 1-1-0, ventral 1-1-2, elsewhere apparently 0; metatarsus dorsal 1-0-0, prolateral only one distal, retrolateral 1-0-0, ventral 0-lp-0-2. Fourth leg: essentially like the third with few exceptions which seem to be unimportant.

Abdomen. 3.25 mm. long; wider than long in ratio of 11 : 10. Other observed features are typical of the genus.

Epigynum. Viewed from a true ventral position, wider than long; with a short scape terminating in a bead-like expansion (Figs. 94-96).

Color in alcohol. Carapace yellowish with brownish dots and reddish flecks on cephalic part; the dots are arranged as a transverse row of four at about the beginning of the posterior declivity and another pair of dots also forming a transverse row in front of the thoracic groove. Sternum light yellow with a few brown flecks. The legs are yellowish with brownish spots and irregular reddish spots on the fourth tibiae and more distal segments. Abdomen: only the anterior end of a dorsal folium persists; most of the dorsum is covered with white subchitinous granules; there

is a paired series of small brown spots in the posterior half of the dorsum which I also regard as remains of the folium; the venter is light colored with white subchitinous granules. In common with other species, the paratypes show a high degree of color variations. In some the folium is well developed, and the legs have many brown spots, rings, and bars. The dots on the carapace appear to be fairly consistent in appearance. In some specimens the venter is dark colored. These facts are added evidence that no great importance can be attached to color patterns in this genus.

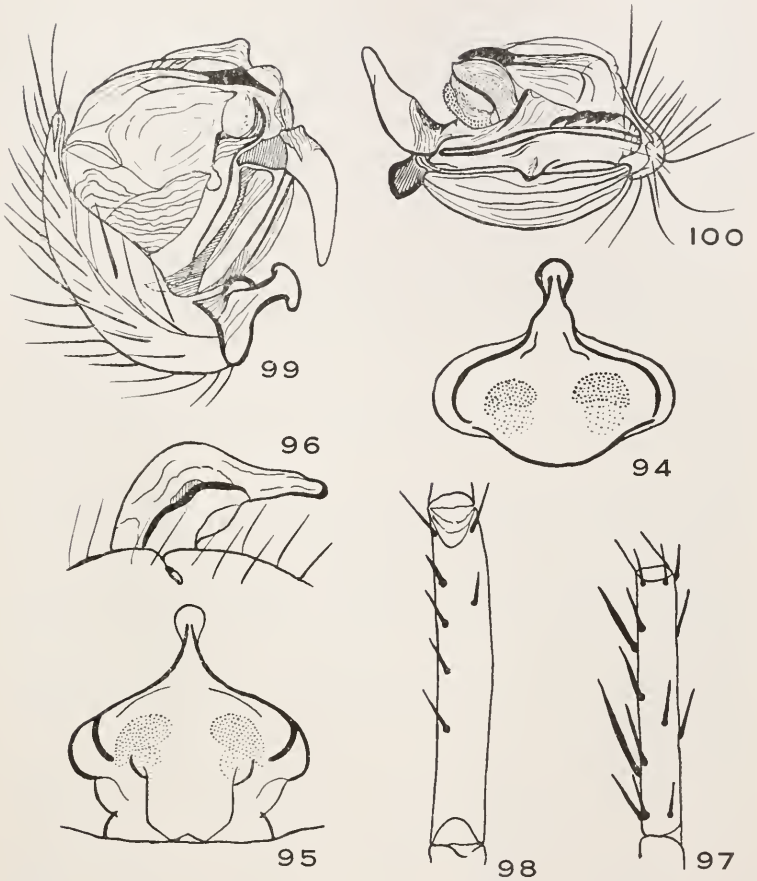
Type locality. The holotype female is from Barro Colorado Island, C. Z., June, 1950. Paratype females from the following localities have been studied: Mante, Mexico, August, 1943; Barro Colorado Island, C. Z., June-July, 1934; June-August, 1936; July-August, 1939; June, 1950; Ft. Randolph, C. Z., August, 1936; France Field, C. Z., August, 1939; Ft. Sherman, C. Z., August, 1939; C. Z. Forest Reserve, C. Z., July-August, 1939; Madden Dam, C. Z., August, 1939; Chilibre, C. Z., July, 1939; Boquete, R. P., July, 1939, August, 1950; El Valle, R. P., July, 1936; Arraijan, R. P., August, 1936; Porto Bello, R. P., August, 1936.

Eustala montana sp. nov.

(Figures 97-100)

Male holotype. Total length 5.395 mm. Carapace 2.665 mm. long; 2.275 mm. wide between second and third coxae where it is widest; .845 mm. tall opposite interval between second and third coxae and, therefore, about .37 as tall as wide; gently inclined from PME to beginning of steep posterior declivity; with well defined median longitudinal thoracic groove; with spines confined to ocular area; covered with a well developed coat of brown and light colored procumbent hair and with a tuft of long white hairs just posterior to PLE.

Eyes. Eight in two rows as usual, all dark; LE on moderately prominent tubercles; viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 19 : 16, wider in front than long in



External Anatomy of *Eustala*
Figures 94-96, *E. minima*
Figures 97-100, *E. montana*

Fig. 94. Epigynum from below.
Fig. 95. Epigynum, a more posterior view.
Fig. 96. Epigynum, lateral view.
Fig. 97. Left second tibia from below.
Fig. 98. Right fourth femur from below.
Fig. 99. Tarsus of male palp, lateral view.
Fig. 100. Tarsus of male palp from distal end.

ratio of 19 : 17. Ratio of eyes AME : ALE : PME : PLE = 11 : 8.5 : 10 : 7.5. AME separated from one another by slightly more than twice their diameter, from ALE by nearly two and one-fourth times their diameter. PME separated from one another by 1.3 times their diameter, from PLE by 3.7 times their diameter. Laterals separated from one another by two-thirds the diameter of PLE. Height of clypeus equal to about 13/11 of the diameter of AME.

Chelicerae. Basal segment .814 mm. long. Fang groove well defined; promargin as usual with four teeth, second and fourth smaller; retromargin with three teeth. Otherwise typical of the genus as far as observed; teeth observed on paratype to avoid injury to holotype.

Maxillae. As usual in the genus in all observed features including the maxillary tooth in opposition to the palpal femoral ridge.

Lip. Wider than long in ratio of about 8 : 5; grooved transversely in basal third; reaches to about the middle of the maxillae. Sternal suture definitely procurved.

Sternum. Scutiform; longer than wide in ratio of 47 : 37; a narrow sclerite continues between fourth coxae which are separated by about one-sixth of their width; with the usual supply of long stiff bristles or spinules.

Legs. 1243. Width of first patella at "knee" .4115 mm., tibial index of first leg 9. Width of fourth patella at "knee" .3357 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.095	1.300	3.445	2.990	1.170	13.000
2.	3.120	1.235	2.405	2.502	1.105	10.367
3.	1.950	.845	1.105	1.040	.650	5.590
4.	2.925	1.202	1.885	2.015	.780	8.807
Palp	.401	.282	.217	——	.909	1.809

Ventral distal retrolateral hook and dorsal tubercle on first coxa together with proximal prolateral ridge and groove on second femur apparently normal for males of the genus.

Spines. First leg: femur dorsal 0-1-0-1-1, prolateral essentially the same, retrolateral 0-0-0-1-1, ventral apparently only one on promargin near distal end and 0-0-0-1-1 on retromargin; patella

dorsal 1(weak)-1, prolateral 0-1-1, retrolateral 0-0-1; tibia dorsal 0-1-0-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-2-lp-lp-2; metatarsus dorsal 0-1-0-0-0, prolateral 0-1-1-0, retrolateral 0-1-0-1-0, ventral lr-lp-lr-lp-0. Second leg: femur as in first except ventral apparently only one on promargin near distal end and four on retromargin, all in distal two-thirds of segment; patella as in first; tibia dorsal 0-1-0-1-1-0, prolateral 1-1-1-0, retrolateral 0-1-1-1, ventral 2-lp-lr-lp-lp-2 (Fig. 97); metatarsus dorsal 0-0-1-0, prolateral 0, retrolateral 0-0-0-1-0, ventral lr-lp-lr-lp-0. Third leg: femur dorsal and prolateral 0-0-1-1-1, retrolateral only one near distal end, ventral three on each margin and all six in distal two-thirds of segment; patella dorsal 0-1-0-1, prolateral and retrolateral 0-1; tibia dorsal 1-0-1-0, prolateral 1-0-1, retrolateral 0-1-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral 1-1-1-1. Fourth leg: femur dorsal as in third, prolateral 0-0-1-1, retrolateral only one near distal end, ventral as shown in Figure 98; patella as in third; tibia dorsal 0-1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-0, ventral 2-lp-lp-2; metatarsus dorsal 0-1-0-1-0, prolateral 0-1-0-1-1, retrolateral 0-0-1-1-0, ventral 0-lp-0-0.

Palp. Complicated; basal femoral ridge, patella, and tibia essentially as in *E. scitula* sp. nov. Tarsus: basal tarsal apophysis a typical, somewhat distorted arrow-head in shape; the clavis is moderately robust, only slightly excavated at its base; the uncus has a very pronounced shoulder at its base and curves around in contact with the conductor as a robust hook; the conductor is large, has a shallow depression to receive the uncus, is finely setose along its anterior surface which is differentiated into a concave and a rounded portion against which the distal end of the embolus is applied; the vesicle is of moderate size and is in the typical position; the embolus appears to have distinctive form best shown in drawings; the terminal laminae have a series of conspicuous sharp carinae, a marked low tubercle, together with a strongly raised portion contiguous to the conductor (Figs. 99-100).

Abdomen. Total length 2.99 mm.; 2.47 mm. wide; with the usual round-triangular form; with the usual supply of long slender dorsal and dorsolateral spinules; other observed features typical of the genus.

Color in alcohol. Carapace yellowish with considerable brownish color in the form of irregular spots and radiations from the thoracic groove; there is a suggestion of a series of dots in a transverse row such as occurs in so many species of the genus; these come out quite clearly in a paratype as a row across at the posterior third of the groove. The sternum is yellowish with a broad grayish margin. The legs are much spotted and banded with brown. Abdomen: there is a well marked brownish dorsal folium; there are three black spots along the dorsolateral regions on each side; the venter has a darker quadrilateral area between the genital groove and the base of the spinnerets but the common central white spot is only barely indicated.

Type locality. The male holotype and a single mature male paratype are both from El Volcan, R. P., August, 1950.

Eustala montivaga sp. nov.

(Figures 101-102)

Female holotype. Total length of 7.80 mm. Carapace 3.185 mm. long; 2.5 mm. wide opposite second coxae where it is widest; .975 mm. tall and, therefore, .39 as tall as wide; median longitudinal thoracic groove moderately well marked but less conspicuous than in some other species of *Eustala;* with a moderately well developed coat of light yellowish hair and numerous short spinules especially on the cephalic region.

Eyes. Eight in two rows, all dark; viewed from above, both rows strongly recurved; viewed from in front, anterior row practically straight, measured by centers; central ocular quadrangle wider in front than behind in ratio of 10 : 9; wider in front than long in ratio of 10 : 9. Ratio of eyes AME : ALE : PME : PLE = 7 : 5 : 6 : 4.5. AME separated from one another by ten-sevenths of their diameter, from ALE by 2.5 times their diameter. PME separated from one another by four-thirds of their diameter, from PLE by about three times their diameter. Laterals separated from one another by slightly less than the diameter of PLE. Height of clypeus equal to four-sevenths of the diameter of AME.

Chelicerae. With basal boss moderately well developed; basal segment 1.17 mm. long; each with long slender bristles in front,

medially directed and overlapping; fang groove well marked and with small dentules; fang groove with four promarginal teeth, the most distal of which is small, and with three retromarginal teeth all fairly robust (on the right side a dentule occurs just external to the most distal normal tooth).

Maxillae. Appear to be entirely typical of the genus.

Lip. Wider than long in ratio of 14 : 9. Sternal suture procurved.

Sternum. Scutiform; moderately convex, especially opposite coxae; scalloped opposite coxae; longer than wide in ratio of 57 : 55; widest between intervals separating second and third coxae but nearly as wide between intervals separating first and second coxae; not continued between fourth coxae which are separated by about one-fourth of their width.

Legs. 1243. Width of first patella at "knee" .484 mm., tibial index of first leg 10. Width of fourth patella at "knee" .44 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.770	1.625	3.445	2.860	1.105	12.805
2.	3.380	1.430	2.860	2.470	1.040	11.180
3.	1.982	.845	1.105	1.105	.780	5.817
4.	3.120	1.310	2.080	2.145	.910	9.565

Spines. In general this species is apparently less spiny than usual in the genus. First leg: femur dorsal 0-1-0-1, prolateral 0-0-1-0-1-1, retrolateral 0-0-0-1-1, ventral 0; patella dorsal 0-1, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 0-1-0-1-1-0, prolateral 0-1-0-1-0, retrolateral 0-0-1-0-1-0, ventral lp-2-2-0-2(two pairs near middle quite irregular); metatarsus dorsal 0-0-1-0, prolateral 0, retrolateral 0-1-1, ventral 2-lp-lr-lp-0. Second leg: femur essentially as in first; patella as in first with spines weak; tibia as in first except ventral 2-2(irregular)-lp-0-2; metatarsus dorsal 0-1-0-0, prolateral 0, retrolateral 0-0-1-0, ventral 2-2(irregular)-lp-0. Third leg: femur dorsal 0-1-1-1, prolateral 0, retrolateral only one near distal end; patella only dorsal 1-1(both weak); tibia dorsal 0-1-0-1-0(both weak), prolateral 0-1-0, retrolateral 0, ventral 1-1-0(both nearly median); metatarsus dorsal 0-1-0, prolateral 0-1-0-1, retrolateral 0, ventral 1-1-1-1(all median). Fourth leg: femur dorsal 0-1-0-1, prolateral apparently 0,

retrolateral only one weak spine near distal end, ventral only two on retromargin near distal end; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-1; tibia dorsal 0-1-1-1-0, prolateral 0-1-1, retrolateral 0-1-1-0, ventral lp-lp-2; metatarsus dorsal 1-1-0, prolateral 0-1-1-1, retrolateral 0-1-0, ventral 0-1-1-1.

Abdomen. With the common round-triangular form and slight suggestions of shoulder humps; 5.53 mm. long; 4.94 mm. wide; with numerous recurved short spinules but apparently no long ones such as occur in other species. Other features essentially typical of the genus.

Epigynum. Similar to that of *E. semifoliata* (O. P. Cambridge) but with certain clear differences (Figs. 101-102). Relatively short and broad; the scape gradually broadens to the base; apertures small and about four diameters of one of them apart; spermathecae a little less than a diameter apart.

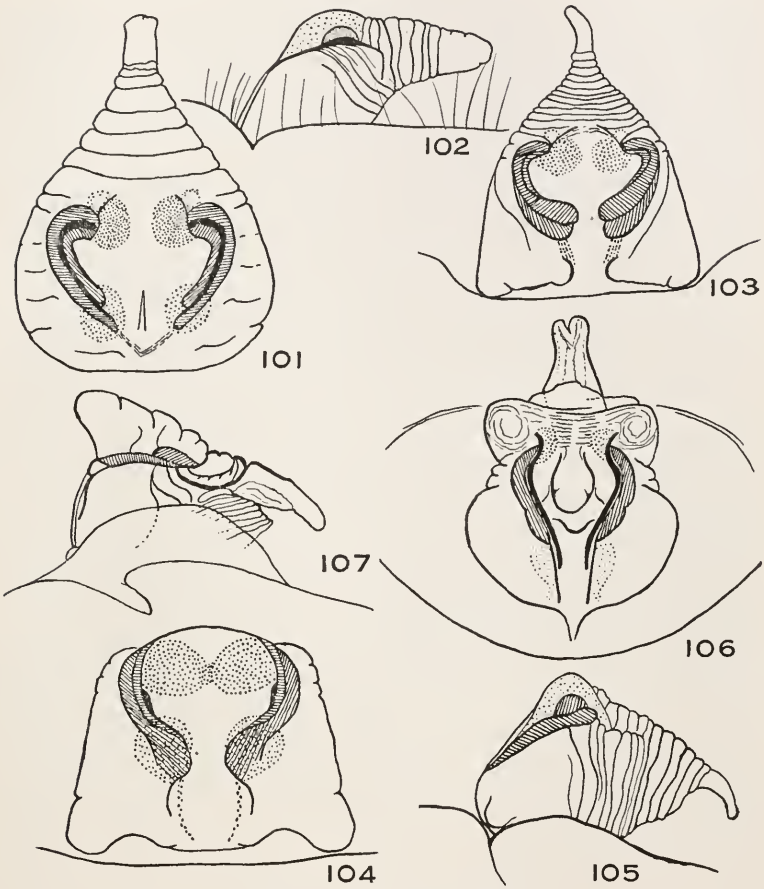
Color in Alcohol. Legs and palps yellowish with large dark brown patches and rings together with smaller spots. Carapace yellowish with four dark dots in two transverse rows in middle of dorsal area (one paratype has these dots arranged in three rows with two in the first, three in the second and four in the third). Sternum dusty yellow with a broad grayish margin. Abdomen: with a moderately distinct brownish dorsal folium; outside of the folium the dorsal and dorsolateral areas are whitish from many subchitinous granules; the venter has a median darker spot with irregular boundaries and whitish patches but without the two conspicuous white spots possessed by *E. semifoliata;* a narrow black ring surrounds the bases of the spinnerets.

Type locality. Female holotype and two smaller but mature female paratypes from El Volcan, R. P., August, 1950.

Eustala panamana sp. nov.

(Figures 103-105)

Female holotype. Total length 5.265 mm. Carapace 2.275 mm. long; 1.82 mm. wide opposite interval between second and third coxae where it is widest; .66 mm. tall opposite second coxae where it is tallest and, therefore, about .36 as tall as wide; rises gradually from PME to highest point and then descends grad-



External Anatomy of *Eustala*
Figures 101-102, *E. montivaga*
Figures 103-105, *E. panamana*
Figures 106-107, *E. redundans*

Fig. 101. Epigynum from below.
Fig. 102. Epigynum, lateral view.
Fig. 103. Epigynum from below.
Fig. 104. Epigynum, a more posterior view.
Fig. 105. Epigynum, lateral view.
Fig. 106. Epigynum from below.
Fig. 107. Epigynum, lateral view.

ually to posterior margin; with well marked median longitudinal thoracic groove and only moderately convex lateral to the groove.

Eyes. Eight in two rows, all dark; viewed from above both rows strongly recurved; viewed from in front, anterior row slightly procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 33 : 30, slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 5.5 : 4 : 5 : 4. AME separated from one another by 18/11 of their diameter, from ALE by twice their diameter. PME separated from one another by seven-fifths of their diameter, from PLE by a little more than three times their diameter. Laterals separated from one another by slightly more than their radius. Height of clypeus nearly equal to the diameter of AME.

Chelicerae. Basal segment .77 mm. long; general features typical of the genus; fang groove well marked and with four promarginal teeth and three retromarginal teeth.

Maxillae. Appear to be completely typical of the genus in all observed features.

Lip. Wider than long in ratio of about 2 : 1; well rounded along distal margin so that the organ is nearly semicircular in outline. Sternal suture procurved.

Sternum. Scutiform; longer than wide in ratio of 6 : 5; moderately convex but with additional convexities opposite all coxae; not continued between fourth coxae which are separated by nearly one third of their width.

Legs. 1243. Width of first patella at "knee" .352 mm., tibial index of first leg 11. Width of fourth patella at "knee" .330 mm., tibial index of fourth leg 15.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.795	.975	2.275	1.690	.845	8.580
2.	2.275	.900	1.755	1.625	.845	7.400
3.	1.495	.583	.780	.780	.640	4.278
4.	2.437	.910	1.397	1.462	.747	6.953

Spines. First leg: femur dorsal 0-1-0-1-1, prolateral 0-0-1-1-1-0, retrolateral 0-0-0-0-1-1, ventral apparently only one on each margin near distal end and both weak; patella dorsal 1-1, prolateral 0-1-0-0, retrolateral 0-0-1-0; tibia dorsal 0-1-1-1-0, prolateral nearly the same, retrolateral 0-1-1-0, ventral lp-0-lp-0;

metatarsus dorsal 0-1-1-1, prolateral only bristles, retrolateral 0, ventral 2-2-0. Second leg: femur dorsal 0-1-0-1, prolateral and retrolateral only one near distal end, ventral apparently only one weak spine on retromargin near distal end; patella as in first; tibia dorsal as in first; prolateral and retrolateral 0-1-0-1-0, ventral 2-lp-lr; metatarsus dorsal 0-1-0-1-0-0, prolateral 0-1-0-1-0, retrolateral 0-1-0-0, ventral 0-lr-0-0. Third leg: femur dorsal 0-1-0-1, prolateral and ventral 0, retrolateral 0-0-1, patella as in first except prolateral 0; tibia dorsal 0-1-0-0, prolateral and retrolateral 0, ventral lp-lp-2; metatarsus dorsal 0-1-1-1, prolateral 0-1-0-0, retrolateral 0-0-1(weak)-0, ventral 1-1-1-1(all median). Fourth leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral apparently one on each margin near distal end and both weak; patella essentially as in first; tibia dorsal 0-1-0-1-0, prolateral 0-1-1-0, retrolateral 0-1-0, ventral lp-lp-2; metatarsus dorsal 0-1-0-1-0-0, prolateral 0-1-1-0, retrolateral 0-1-0-0, ventral 0-0-1 (median). Tarsal claws as usual in the genus. Palpal claw long, slender, gently curved; pectinate in a single row of about nine teeth increasing in length distally.

Abdomen. With the usual round-triangular form but more rounded than usual; 3.282 mm. long; 3.25 mm. wide at greatest width about one fourth from base; high as well as relatively broad; with a moderate supply of long spinules; other features appear to be typical of the genus.

Epigynum. Relatively broad; with scape gradually narrowed from base to tip which is not rugulose like the broader part; the apertures are three to four diameters apart; the spermathecae are close together and when viewed from a posterior position seem to be in contact; the oval part of the base is prominent (Figs. 103-105).

Color in alcohol. Legs and mouth parts generally yellowish with dark spots of various sizes. Carapace: yellowish with considerable dusty gray over the cephalic area; this extends back as a median stripe through most of the length of the median thoracic groove; the cephalic area has a more or less V-shaped, white spot caused by an accumulation of subchitinous granules; there is a black dot on each side just in front of the median groove and a transverse row of four black dots at about the middle of the groove. The lip is white in the middle at the base but gray else-

where. The sternum is light grayish with irregular white subchitinous spots and opposite each coxa there is a much darker rounded spot. Abdomen: nearly white from a large number of angular subchitinous granules; with a faintly outlined dorsal folium; there is an elongated white spot just behind the genital groove and this is bordered by a short narrow, nearly black stripe on each side.

Type locality. The holotype is from Cerro Punta, Chiriqui, R. P., March, 1936 (W. J. Gertsch). There are two mature female paratypes and what I assume to be an immature male from the same locality and probably collected at the same time.

Eustala redundans sp. nov.

(Figures 106-107)

Female holotype. With the conventional round-triangular form. Total length 6.175 mm. Carapace 2.41 mm. long; 2.08 mm. wide opposite interval between second and third coxae where it is widest; .968 mm. tall and, therefore, about .47 as tall as wide; median longitudinal thoracic groove well defined; with numerous short brown spinules especially on the cephalic part together with a moderately well developed coat of light colored procumbent hair.

Eyes. Eight in two rows, all dark as usual; viewed from above, posterior row strongly recurved; viewed from in front, anterior row definitely procurved; central ocular quadrangle wider in front than behind in ratio of 11 : 9, wider in front than long in ratio of 33 : 29. Ratio of eyes AME : ALE : PME : PLE = 9 : 7.5 : 9.5 : 8. AME separated from one another by twice their diameter, from ALE by slightly more than three times their diameter. PME separated from one another by about 6/5 of their diameter, from PLE by a little more than four times their diameter. Laterals separated from one another by 2/3 of the diameter of ALE. Height of clypeus equal to a little more than the diameter of AME.

Chelicerae. Basal segment .877 mm. long; general features agree well with the typical species of the genus. The fang groove is well defined and provided with the usual sets of teeth, four on promargin and three on retromargin.

Maxillae. Appear to be typical of the genus in all observed features.

Lip. Wider than long in ratio of about 5 : 4; reaches to somewhat beyond the middle of the maxillae. Sternal suture distinctly procurved.

Sternum. Scutiform; longer than wide in ratio of about 9 : 8; not continued between fourth coxae which are separated by a little less than one-fifth of their width; with low convexities opposite each coxa; with the usual supply of long stiff bristles.

Legs. 1243. Width of first patella at "knee" .4007 mm., tibial index of first leg 10. Width of fourth patella at "knee" .3899 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.380	1.170	2.925	2.740	.975	11.190
2.	2.925	1.170	2.340	2.275	.747	9.457
3.	1.885	.750	1.040	1.007	.682	5.364
4.	2.860	1.170	1.787	1.820	.785	8.422

Spines. First leg: femur dorsal 0-1-0-1-1, prolateral 0-0-1-1-1-0, retrolateral 0-0-0-1-1-0, ventral apparently only one on retromargin near distal end; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-1-1-1, ventral 2-2-2-0-0 with considerable irregularity; metatarsus dorsal 0-1-1-0, prolateral 0, retrolateral 0-1-1-0, ventral 2-2-lp-0-0. Second leg: femur essentially as in first except ventral 0; patella as in first except right prolateral 0-1-1; tibia as in first except ventral lr-2-lr-lp-lr-lr(last two weak); metatarsus dorsal 0, prolateral 0-1-1-1-0, retrolateral essentially the same, ventral 0-lp-lr-0-0. Third leg: femur dorsal as in first, prolateral and retrolateral only one near distal end, ventral 0 but spinules in rows suggest reduced spines; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0; tibia dorsal 1-0-0, prolateral 0-1-0, retrolateral 0, ventral lp-lp-2(weak); metatarsus dorsal 0-1-1-0, prolateral and retrolateral 0-1-0, ventral lp-lp-lp-2 (weak). Fourth leg: femur as in third except ventral one on retromargin near distal end; patella dorsal and prolateral as in third, retrolateral 0-0-1; tibia dorsal as in third, prolateral 1-1-1-1, retrolateral 0-1-1, ventral lp-lp-lp-2; metatarsus dorsal 0-1-1-0-0, prolateral 0-1-0-1-1, retrolateral 0, ventral lp-0-0-1.

Abdomen. 3.77 mm. long; 3.77 mm. wide at its widest place about one-fifth from base; with the usual round-triangular form. Other observed features appear to be typical of the genus.

Epigynum. Quite distinctive; apertures nearly three diameters apart; scape of moderate length and arises abruptly from base and appears bifid at its tip; the central part of base with a strongly developed postero-ventral projection different from that in any other known species (Figs. 106-107).

Color in alcohol. Carapace: pars thoracica mostly yellowish; the two rows of dots which so frequently appear in these species are present and in addition there is a brownish bar extending forward and laterally parallel to the cephalic groove; the latter is speckled with brown. The sternum is yellowish with grayish marginal spots covering the convexities. The legs are yellowish with many brown dots, larger spots, bars, and rings. Abdomen: the dorsal folium is moderately well outlined and extends forward as a narrow extension; near the middle of the dorsum there is an oval purplish spot, probably an individual mark; the remainder of the dorsum and dorsolateral regions is darkly colored from a combination of brown pigment, subchitinous yellowish-white granules in the form of dots, streaks, and larger irregular spots; the venter has a large quadrilateral area between the genital groove and base of the spinnerets containing an elongate oval white spot.

Type locality. The holotype is from Madden Dam Forest, C. Z., July, 1950. There are no paratypes.

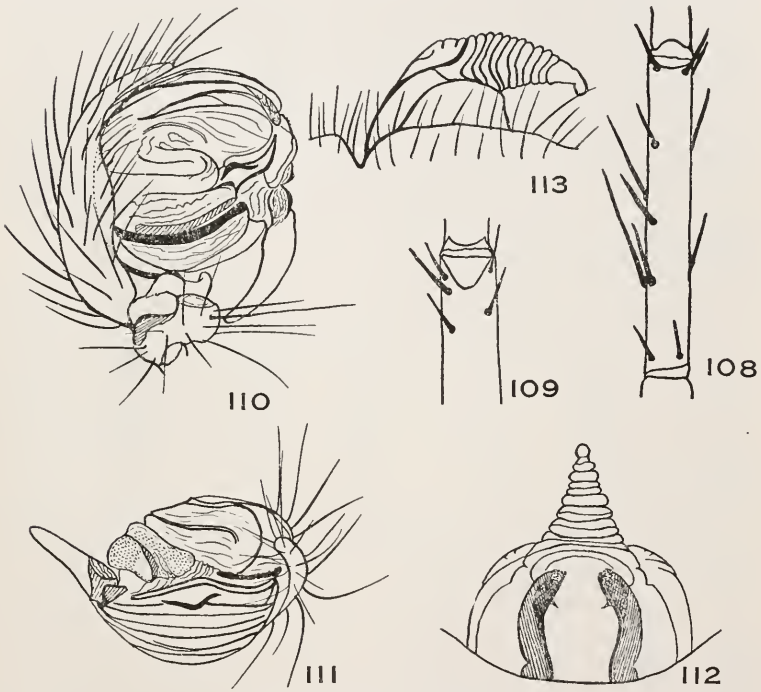
Eustala rustica sp. nov.

(Figures 108-113)

Male holotype. Total length 4.03 mm. Carapace 2.068 mm. long; 1.716 mm. wide opposite interval between second and third coxae where it is widest; .78 mm. tall and, therefore, about .45 as tall as wide; gently inclined from PME to beginning of steep posterior declivity; with well defined median longitudinal thoracic groove; with spines confined to ocular area; with a moderately well developed coat of light colored procumbent hair.

Eyes. As usual, eight in two rows, all dark; LE on moderately prominent tubercles; viewed from above, posterior row strongly

recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 19 : 16, wider in front than long in ratio of 19 : 16. Ratio of eyes AME : ALE : PME : PLE = 12 : 9 : 11 : 8. AME separated from one another and from ALE by their diameter. PME separated from one another by slightly more than their diameter, from PLE by a little less than three diameters. Laterals separated from one another by one-third of



External Anatomy of *Eustala*
Figures 108-113, *E. rustica*

Fig. 108. Left second tibia of male from below.
Fig. 109. Distal half of right fourth femur from below.
Fig. 110. Tarsus of male palp, lateral view.
Fig. 111. Tarsus of male palp from distal end.
Fig. 112. Epigynum from below.
Fig. 113. Epigynum, lateral view.

the diameter of ALE. Height of clypeus equal to about the diameter of AME.

Chelicerae. Basal segment .594 mm. long. Fang groove well defined; promargin with four teeth, second and fourth smaller; retromargin with three teeth. Otherwise as usual and typical of the genus in all observed features.

Maxillae. As usual in the genus in all observed features including the maxillary tooth used in opposition to the palpal femoral ridge.

Lip. Only slightly wider than long; moderately grooved and transversely striated in basal half; reaches to about the middle of the maxillae. Sternal suture gently procurved.

Sternum. Scutiform; longer than wide in ratio of about 5 : 4; a narrow sclerite continues between fourth coxae which are barely separated; with the usual supply of long slender spinules.

Legs. 1243. Width of first patella at "knee" .2924 mm., tibial index of first leg 8. Width of fourth patella at "knee" .2491 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.315	1.108	2.665	2.275	.990	10.350
2.	2.600	.812	1.885	1.950	.910	8.157
3.	1.540	.528	.814	.902	.550	4.334
4.	2.405	.858	1.254	1.755	.780	7.052
Palp	.418	.253	.132	——	.792	1.595

Ventral distal retrolateral hook on first coxa, dorsal tubercle on first coxa, and prolateral proximal ridge and groove on second femur all well developed.

Spines. First leg: femur dorsal and prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1, ventral 0-0-1-0-1 on promargin and only one on retromargin near distal end; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-1-1; tibia dorsal 0-1-0-1-1-0, prolateral 0-1-0-1-0, retrolateral essentially the same, ventral 2-2-2-lp-2 with some irregularity; metatarsus dorsal 0-1-0-1-0-0, prolateral 0-1-0, retrolateral 0-1-1-0, ventral lr-2-0-0. Second leg: femur dorsal as in first, prolateral and retrolateral 0-0-0-1-1, ventral apparently only one near middle on retromargin but lacking on right; patella dorsal as in first, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0, retrolateral 0-1-1-1, ventral

2-lp-lp-lp-2 (Fig. 108) ; metatarsus dorsal 0-1-0-1-0-0, prolateral 0, retrolateral 0-1-0-1-0, ventral 0-2-lp-0. Third leg : femur dorsal as in first, prolateral and retrolateral only one near distal end, ventral three on promargin all in distal half and one on retromargin near distal end ; patella dorsal and prolateral as in first, retrolateral 0-1-0 ; tibia dorsal 0-1-0-0, prolateral and retrolateral 0-1-1, ventral 0-lp-0-2 ; metatarsus dorsal 0-1-1-0, prolateral 0-1-1, retrolateral 0, ventral 2?-lp-lp-lp. Fourth leg : femur dorsal as in first, prolateral 0-0-0-1-1, retrolateral only one near distal end, ventral two on promargin and three on retromargin (four on retromargin of left femur), all in distal third of segment (Fig. 109) ; patella as in third ; tibia dorsal 1-1-1-0, prolateral 0-1-1-1, retrolateral 0-1-1, ventral 2-lp-lp-2 ; metatarsus dorsal 0-1-0-0, prolateral 0-1-1-1, retrolateral 0-1-1-0, ventral 0-lp-0-0. Ventral distal retrolateral hook and dorsal tubercle on first coxa well developed ; proximal prolateral groove and ridge on second femur well defined.

Palp. Complicated ; basal femoral ventral ridge, patella, and tibia all typical of the genus. Tarsus : basal tarsal apophysis as usual a somewhat distorted arrow-head in shape ; the clavis is moderately robust, not notably excavated at its base but with a groove and sharp ridge ; the uncus is a rather slender long pointed hook with a rounded shoulder at its base ; the conductor is of moderate size, with a ventral depression for the reception of the uncus and a moderately deep depression on its anterior surface where it is finely setose ; the vesicle is of moderate size and in its typical position ; the embolus is robust, grooved into a trough, its free part is short and accompanied by a membrane ; the terminal laminae are not strikingly differentiated but there is a thin chitinous extension at the base of the clavis (Figs. 110-111).

Color in alcohol. Both known male specimens of this species are light colored. The carapace is bright yellowish with a few pale brownish dots ; one pair of these occurs at the middle of the thoracic groove ; another pair of larger dots lies at the base of the pars cephalica and a third pair about halfway between PME and the anterior end of the thoracic groove. The sternum is yellowish with gray flecks around the margin. The legs are yellowish with pale brownish bars, rings, and spots. Abdomen :

a well developed dorsal folium exists but elsewhere dorsally and dorsolaterally this part of the body is white from the accumulation of many subchitinous granules; there is a small central white spot with a dark irregular spot on each side of this in the area between the genital groove and the base of the spinnerets. The paratype agrees well with the holotype except that there is more color on the carapace.

Although certainty is lacking, I think the evidence is sufficient to allow the pairing of the females described below with males already described as *E. rustica* sp. nov. The specimen selected as the allotype is somewhat distorted by preservation but is in good condition otherwise.

Female allotype. Total length 5.72 mm. Carapace 2.275 mm. long; 1.82 mm. wide opposite interval between second and third coxae where it is widest; .975 mm. tall and, therefore, about .54 as tall as wide; steep posterior declivity somewhat more pronounced than in male.

Eyes. Central ocular quadrangle only slightly wider in front than behind; only slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 11 : 8 : 11 : 7.5. AME separated from one another by about one and one-quarter times their diameter, from ALE by nearly twice their diameter. PME separated from one another by slightly more than their diameter, from PLE by three times their diameter. Laterals separated from one another by slightly more than the radius of ALE. Height of clypeus equal to slightly less than the diameter of AME.

Chelicerae. Basal segment .758 mm. long. Otherwise essentially as in male.

Maxillae. Apparently as in male in all essential features.

Lip. Wider than long in ratio of 4 : 3. Otherwise essentially as in male.

Sternum. Longer than wide in ratio of 40 : 37. The spinules show more clearly than in male; these consist of many short spinules and longer and more robust ones situated as follows: at the posterior end there is a group of four; opposite each of the coxae except the fourth there is a pair; in addition to these four others make a nearly transverse row between the first coxae. Similar spinules were probably present in the male before

handling and agitation in the vials. Otherwise essentially as in the male.

Legs. 1243. Width of first patella at "knee" .3682 mm., tibial index of first leg 10. Width of fourth patella at "knee" .3249 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.120	1.170	2.535	2.080	.942	9.847
2.	2.567	1.040	2.080	1.787	.845	8.319
3.	1.495	.660	.858	.942	.617	4.572
4.	2.372	.845	1.690	1.657	.780	7.344

Spines. First leg: femur dorsal 0-1-0-1, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1, ventral 0; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-1-1; tibia dorsal 0-1-0-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-lp-lp-0-lr; metatarsus dorsal 0-1-0-1-0-0, prolateral 0, retrolateral 0-1-0-1-0, ventral 0-2-lp-0. Second leg: femur as in first except prolateral 0-0-0-1-1; patella as in first; tibia as in first except ventral 2-lp-0-2; metatarsus as in first except ventral lr-2-lp-0-0. Third leg: femur dorsal as in first, prolateral and retrolateral only one near distal end, ventral spinules probably not to be regarded as spines; patella apparently only dorsal 1-0, tibia dorsal 1-0-0, prolateral 0, retrolateral 0-0-1, ventral lr-lr-2; metatarsus dorsal 0-1-1-0, prolateral and retrolateral 0-1-0, ventral lp-lp-lp-lp. Fourth leg: femur as in third except ventral one on promargin near distal end; patella dorsal 1-0, prolateral 0-1; tibia dorsal and prolateral 0-1-0-1-0, retrolateral 0-1-0, ventral lp-0-2; metatarsus dorsal and prolateral 0-1-0-1-0, retrolateral 0, ventral 0-0-1. Palp: with fewer spines and spinules than is usual in the genus.

Abdomen. 3.77 mm. long; 3.445 mm. wide about one-fourth from base. Apparently with slightly indicated shoulder humps. Otherwise essentially as in male.

Epigynum. Base broad; scape of moderate length and gradually narrowed to tip. Apertures small and about two diameters apart. The central conspicuous part of the base relatively narrow and longer than usual. Tip of scape turned dorsally (Figs. 112-113). Figure 113 is from the paratype because the base is more completely expanded and shows in profile to much better advantage.

Color in alcohol. The female allotype is much more deeply colored than the male holotype or the single female paratype. The carapace lacks the dots but nearly the whole pars cephalica is brown; there is also a pair of brownish bands each reaching out from the thoracic groove a little posterior to the pars cephalica. Abdomen: the dorsal folium is well developed; there is a pair of small white dorsal dots near the base; the numerous white granules so conspicuous in the males are nearly all obscured in the female allotype; the venter is like that of the male except that there is more of the dark brown color.

Type locality. The holotype male and the allotype female are from El Valle, R. P., July, 1936. Paratypes of both sexes are in the collection from the same locality and collected at the same time.

Eustala scitula sp. nov.

(Figures 114-117)

Male holotype. Total length 5.525 mm. Carapace 3.055 mm. long; 2.535 mm. wide opposite interval between second and third coxae where it is widest; 1 mm. tall opposite third coxae and, therefore, about .4 as tall as wide; rises considerably but gradually to beginning of steep posterior declivity; with well developed median longitudinal thoracic groove; spines confined to ocular area.

Eyes. As usual, eight in two rows, all dark; LE tubercles less prominent than in many species of the genus; viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 42 : 33; wider in front than long in ratio of 21 : 19. Ratio of eyes AME : ALE : PME : PLE = 13 : 8.5 : 11 : 8.5. AME separated from one another by about five-thirds of their diameter, from ALE by a little more than twice their diameter. PME separated from one another by a little more than their diameter, from PLE by a little less than four times their diameter. Laterals separated from one another by a little more than their radius. Height of the clypeus equal to a little more than the diameter of AME.

Chelicerae. Basal segment .780 mm. long. Fang groove well defined; promargin with four teeth, second and fourth smaller as usual; retromargin with three teeth but two and four have been found among the paratypes which were examined to avoid injury to the holotype; weaker than usual in males of the genus.

Maxillae. In general, as usually found in the genus, including the lateral tubercle or tooth used in opposition to the palpal femoral ridge.

Lip. Only slightly wider than long; reaches to about the middle of the maxillae. Basal half moderately grooved. Sternal suture definitely procurved.

Sternum. Scutiform; longer than wide in ratio of about 5 : 4; a narrow sclerite continues between fourth coxae which are barely separated; rather deeply scalloped opposite all coxae; probably with few bristles or spinules in life.

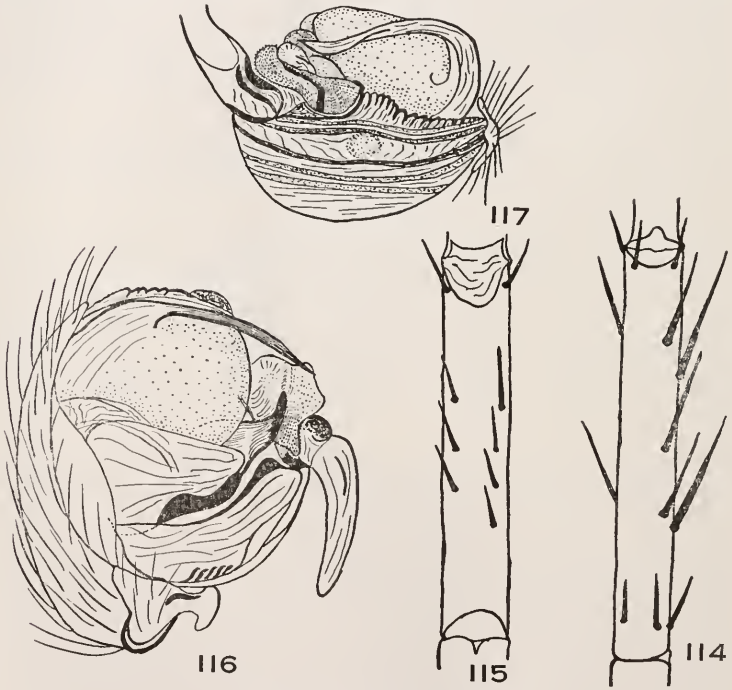
Legs. 1243. Width of first patella at "knee" .444 mm., tibial index of first leg 8. Width of fourth patella at "knee" .4115 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	4.680	1.365	3.900	3.250	1.300	14.495
2.	3.445	1.235	2.535	2.730	1.170	11.115
3.	2.080	.780	1.105	1.105	.650	5.720
4.	3.315	1.300	2.210	2.470	1.050	10.345
Palp	.466	.325	.184	——	.940	1.915

First coxae with the usual well developed ventral distal retrolateral hook and the dorsal tubercle; prolateral groove and ridge on second femur also well developed.

Spines. First leg: femur dorsal 0-0-1-1-1, prolateral left 0-0-1-1-1-1-1, right 0-0-1-2-0-1, retrolateral 0-0-1-1-1, ventral with several irregularities not recorded; patella dorsal 0-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-0-1-1-0, prolateral 0-1-0-1-1, retrolateral 0-0-1-1-0, ventral 2-2-2-2-2; metatarsus dorsal 0-1-0-1-0-0, prolateral 0, retrolateral 0-0-1-1-0, ventral 2-lp-lr-lp-0. Second leg: femur dorsal 0-1-1-1, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1, ventral four on retromargin and apparently only one on promargin near distal end; patella as in first; tibia dorsal essentially as in first, prolateral 1-1-1-0, retrolateral 0-1-1-1, ventral 2-lp-lp-lp-2 (Fig. 114); metatarsus dorsal 0-1-0, pro-

lateral 0-1-1-0, retrolateral the same except for minor differences in position, ventral lr-lr-0-0. Third leg: femur dorsal 0-0-1-1-1, prolateral and retrolateral 0-0-0-1-1, ventral three on promargin and two on retromargin; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-0-1-0, prolateral and retrolateral 0-1-1, ventral lp-lp-lp-2 (second lacking on right); metatarsus dorsal 0-1-0, prolateral 0-1-1, retrolateral 0-1-0, ventral 1-1-1-1. Fourth leg: femur dorsal and prolateral as in third, retrolateral only one near distal end, ventral four on promargin and five on retromargin (Fig. 115), all in distal three-fourths of



External Anatomy of *Eustala*
Figures 114-117, *E. scitula*

Fig. 114. Right second tibia from below.
Fig. 115. Left fourth femur from below.
Fig. 116. Tarsus of male palp, lateral view.
Fig. 117. Tarsus of male palp from distal end.

segment; patella as in third; tibia dorsal 1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-1, ventral 2-lp-lp-2; metatarsus dorsal 1-0-1-0, prolateral and retrolateral 0-1-1-0, ventral 0-lp-lp-1 (weak).

Palp. Complicated; basal femoral tubercle or ridge opposing the maxillary tooth well developed; patella short, with the usual weak dorsal proximal spine or spinule and the long slender distal dorsal spine; the tibia is also short and distinctly trilobed, the chitinous ventral rim of the articular lobe well developed; the femur has a well developed dorsal distal spine. Tarsus: the basal tarsal apophysis has the typical distorted arrowhead shape; the clavis is fairly robust and has a small shallow concave surface at its base; the uncus is a robust spine fitting into a very narrow depression in the conductor; the conductor is a massive structure with a narrow longitudinal groove on its ventral surface and a fairly deep depression and related surfaces on its distal end which is extensively setose; the vesicle is large and occupies the typical position; the embolus is fairly long and moderately slender; the terminal laminae are much wrinkled and strongly chitinized (Figs. 116-117).

Abdomen. Total length 3.25 mm.; 2.405 mm. wide; with the usual round-triangular form; with the usual supply of long slender dorsal and dorsolateral spinules; other observed features typical of the genus.

Color in alcohol. The general color of the carapace is yellowish; behind PME there is a pair of pale brownish spots somewhat elongated; the remainder of the dorsal part of the carapace is covered with an irregular brownish spot; the dots, so commonly present, do not show in the holotype and very seldom among the paratypes. The sternum is yellowish irregularly margined in gray. Legs: generally yellowish but with anterior femora brown in the distal three-fourths; the second and fourth femora are essentially like the first; all segments distal to the patellae are banded with brown. Abdomen: the dorsal folium is well developed but differs greatly among the paratypes; the most persistent features appear to be an oval white spot set into the middle of the usual dark ventral area between the genital groove and base of the spinnerets, but this may be almost circular in shape in certain paratypes.

Type locality. The holotype is from Barro Colorado Island, C. Z., July, 1950. Male paratypes have been collected from the following localities: Barro Colorado Island, C. Z., June-August, 1936; March, 1936 (Gertsch); August, 1939; July, 1950; Canal Zone Forest Reserve, C. Z., August, 1936 and July, 1939; Summit, C. Z., July-August, 1950. One specimen from near Hidalgo, Mexico, July, 1936 (Davis) and another from Cuyutlan, Colima, Mexico, January, 1943 (F. Bonet) are somewhat hesitantly assigned to the species.

Eustala scutigera (O. P. Cambridge)

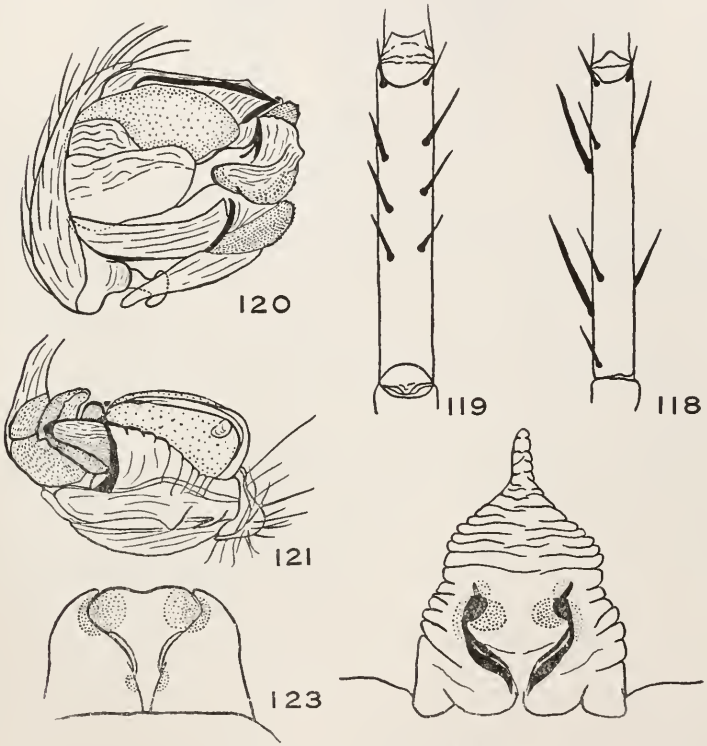
(Figures 118-123)

Epeira scutigera O. P. Cambridge, 1898
E. nava O. P. Cambridge, 1899
Eustala scutigera F. P. Cambridge, 1904
Epeira scutigera Banks, 1909
Eustala scutigera Petrunkevitch, 1911
E. s. Petrunkevitch, 1925

Considerable doubt has hitherto existed as to the identification of this species. The figures published by the Cambridges are not as revealing and definite as desired. The male from the British Museum has a clearly lobed conductor as suggested by F. P. Cambridge's figure. The chief difficulty now arises from the fact that another male from the British Museum labelled *E. guttata* also has an identically lobed conductor and other features like this species. The conclusion that the Cambridges were, at least in this instance, using mixed material seems inescapable. It is also difficult to separate females from those of *E. vegeta* (Keyserling). About the only way to separate them is by using the features of the epigynum; in *E. vegeta* the apertures are further apart than in *E. scutigera* and there are differences in the way in which the scape arises from the base.

Male hypotype. Total length 3.965 mm. With the abdomen round-triangular as usual. Central ocular quadrangle wider in front than behind in ratio of 34 : 29, slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 12 : 8.5 : 9.5 : 8.5. AME separated from one another by seven-sixths of their diameter, from ALE by four-thirds of their diameter.

PME separated from one another by slightly more than their diameter, from PLE by about three times their diameter. Laterals separated from one another by about one-third of their diameter. A pair of long slender spines arises between AME and PME; and another similar spine arises just behind PLE. Height of clypeus equal to the diameter of AME. Promargin of



External Anatomy of *Eustala*
Figures 118-123, *E. scutigera*

Fig. 118. Left second tibia from below.
Fig. 119. Left fourth femur from below.
Fig. 120. Male palpal tarsus, lateral view.
Fig. 121. Male palpal tarsus from distal end.
Fig. 122. Epigynum from below.
Fig. 123. Epigynum, a more posterior view.

fang groove with four teeth; retromargin with three. The secondary sexual characters on the maxillae, first coxae, and second femora appear as usual.

Legs. 1243. Width of first patella at "knee" .2924 mm., tibial index of first leg 8. Width of fourth patella at "knee" .2383 mm., tibial index of fourth leg 9.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.380	1.072	2.535	2.145	.877	10.009
2.	2.730	.950	1.950	1.852	.845	8.327
3.	1.430	.520	.910	.812	.520	4.192
4.	2.275	.910	1.560	1.560	.715	7.020
Palp	.433	.173	.162	——	.770	1.538

The important spination of the second tibia is shown in Figure 118. The first femur appears to have no ventral spines; the second femur has a short robust spine on the retromargin a little distal to the middle and a pair of weak spines near the distal end; the third femur has three fairly robust ventral spines on the promargin; the fourth femur has a double series of ventral spines with four robust spines on each margin (Fig. 119). Considerable variation in spination has been noted among my specimens.

Palp. It seems reasonably certain from F. P. Cambridge's figure and the specimens from the British Museum that this is the species named *Epeira scutigera* by the elder Cambridge. Features of femora, patellae, and tibiae apparently typical of the genus. Tarsus: basal tarsal apophysis a twisted arrow-shape; clavis moderately robust, with a long basal articular surface contiguous to the conductor but not excavated; the uncus is a robust hook, broad at its base and with its tip somewhat recurved; the conductor is hollowed out for the reception of the uncus and provided with a distinct setose lobe; the vesicle is moderately large; the embolus is relatively long and nearly straight along its distal border from the basal elbow to the tip; the terminal laminae show a very conspicuous elevation and together with the conductor show several distinctive surfaces (Figs. 120-121). Degrees of chitinization and folding of the parts in the resting condition alter to some extent the appearance of some of these parts and make it difficult to place certain individuals in the collection.

Female hypotype. Total length 4.68 mm. With the same general form as in the male.

Legs. 1243. Width of first patella at "knee" .3249 mm., tibial index of first leg 10. Width of fourth patella at "knee" .2816 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.990	1.105	2.080	1.852	.747	8.774
2.	2.405	1.007	1.690	1.852	.747	7.701
3.	1.365	.590	.715	.747	.585	4.002
4.	2.145	.975	1.365	1.300	.650	6.435

Ventral femoral spines appear to be rather uniformly lacking in females but may occasionally occur.

Epigynum (Figs. 122-123). The base is massive with the scape abruptly narrowed in its terminal third; apertures more than their width from the lateral side of the epigynum and about three diameters apart; spermathecae one diameter apart; closely resembles that of *E. vegeta.*

Color in alcohol. As usual the color pattern is extremely variable. In both sexes there are two transverse rows of small brownish dots across the carapace; the folium is clear in both hypotypes but may be lacking in some specimens; in both hypotypes the venter has a somewhat elongated central white spot in the middle of a dark area which is margined by incurved white marks; the central white spot appears to be more persistent than the other marks; the sternum is usually yellowish with marginal brown spots opposite the coxae.

Type locality. Male hypotype from Barro Colorado Island, C. Z., July, 1936; the female hypotype is from the same locality, August, 1939. Males and females from Mexico: Cerro Azul, Vera Cruz, March, 1945 (E. K. Waering); Mapastepec, Chiapas, June-July, 1940 (H. Wagner); Teotitlan, Oaxaca, Sept., 1944 (H. Wagner); Papanto, Vera Cruz, October, 1947 (H. Wagner). Guatemala: Patulul, January, 1912 (W. M. Wheeler); Antigua, August, 1947 (C. & P. Vaurie). Nicaragua: Granada (C. F. Baker), Honduras: Subirana, Yoro, (Stadelman). Panama: Barro Colorado Island, C. Z., June-August, 1936; July-August, 1939; June-July, 1950; El Valle, July, 1936; Porto Bello, August, 1936; Ft. Sherman, C. Z., August, 1939; Boquete, July, 1939 and August, 1950.

Eustala sedula sp. nov.
(Figures 124-126)

Female holotype. Total length 6.89 mm. Carapace 2.925 mm. long; 2.6 mm. wide opposite interval between second and third coxae where it is widest; .975 mm. tall and, therefore, about .38 as tall as wide; median longitudinal thoracic groove well defined and typical of the genus; with well developed coat of yellowish white procumbent hair and numerous spinules especially on the pars cephalica.

Eyes. Eight in two rows, all dark as usual; viewed from above, posterior row definitely recurved; viewed from in front, anterior row definitely procurved; central ocular quadrangle as wide behind as in front, wider than long in ratio of 11 : 10. Ratio of eyes AME : ALE : PME : PLE = 12 : 9 : 13.5 : 10.5. AME separated from one another by seven-fourths of their diameter, from ALE by slightly more than two and one-half times their diameter. PME separated from one another by a little less than one and one-half times their diameter, from PLE by a little less than three and three-fourths times their diameter. Laterals separated from one another by two-thirds of the diameter of PLE. Height of clypeus equal to the diameter of AME.

Chelicerae. Basal segment 1.105 mm. long; fang groove well defined and with the usual complement of teeth on both margins; other observed features typical of the genus.

Maxillae. Appear to be completely typical of the genus in all observed features.

Lip. Wider than long in ratio of about 23 : 19; gently grooved and cross striated in proximal third. Sternal suture definitely procurved; with marked anterolateral sternal tubercles at lateral ends of suture.

Sternum. Scutiform; longer than wide in ratio of 29 : 25; with a bluntly bifurcated posterior end which is not continued between fourth coxae which are separated by about one-quarter of their width; only moderately convex opposite the coxae; with a moderately well developed supply of long and short bristles and with a row of six spinules between first coxae.

Legs. 1243. Width of first patella at "knee" .4657 mm., tibial index of first leg 10. Width of fourth patella at "knee" .4332 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.510	1.495	3.022	2.665	1.170	11.862
2.	3.315	1.495	2.567	2.600	1.040	11.017
3.	2.275	.925	1.170	1.300	.780	6.450
4.	2.990	1.365	2.015	2.210	.910	9.490

Spines. First leg: femur dorsal 0-0-1-0-1, on right and 0-0-0-0-1 on left, prolateral 0-0-1-1-1 on right and 0-1-1-1-1 on left, retrolateral 0-0-0-1-1, ventral only one on promargin and retromargin near distal end; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0-0-1-1-1 on left and 0-1-0-1-1 on right, ventral 2-lp-lp-0-2; metatarsus dorsal 0-1-1-0-0, prolateral 0, retrolateral 0-1-0-0, ventral 2-2-2-0. Second leg: femur dorsal 0-0-1-1-1 on right and 0-0-1-0-1 on left, prolateral 0-0-1-1-1, retrolateral 0-0-0-1-1 on right and only one near distal end on left, ventral 0; patella essentially as in first; tibia dorsal as in first, prolateral and retrolateral 0-1-0-1-1, ventral 2-lp-lp-lr; metatarsus dorsal 0-1-1-0, prolateral 0-1-1-0, retrolateral 0-1-0-1-0, ventral 2-2-lp-0. Third leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral 0; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0; tibia dorsal 1-0-1-0, prolateral 0-1-0, retrolateral 0-0-1, ventral lp-lp-2; metatarsus dorsal 0-1-0, prolateral 0-1-1, retrolateral 0, ventral lp-0-1-1. Fourth leg: femur essentially as in third except ventral one on retromargin near distal end; patella as in third except retrolateral 0-0-1; tibia dorsal 0-1-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-0, ventral lp-lp-2; metatarsus dorsal 1-1-0, prolateral 0-1-0-1-1, retrolateral 0-1-1-0, ventral 0-lp-lp-lp.

Abdomen. 4.03 mm. long; 3.51 mm. wide between possible suppressed shoulder humps nearly one-third of length from base; with the usual round-triangular form; also with just the suggestion of a dorsoventral bifid condition similar to that found in *E. bifida;* other observed features appear to be normal to the genus.

Epigynum. The scape is very long as compared to the width of the base; the central part of the base is very prominent; the apertures are very close together; the internal tubules appear to present a rather characteristic pattern (Figs. 124-126).

Color in alcohol. The carapace is generally yellowish; the

pars cephalica has a central darker patch behind the PME and a pair of similar dorsal patches at the base of this region; there is also an irregular whitish spot halfway between PME and the thoracic groove made by an accumulation of white subchitinous granules. The legs are, as usual, yellowish with brown rings and spots. Abdomen: isolated parts of the dorsal folium remain in the holotype but the dorsum and lateral sides are largely yellowish-white from an accumulation of subchitinous granules; the venter has a large brownish, somewhat quadrilateral area, between the genital groove and the base of the spinnerets containing a rounded central white spot. In some paratypes the carapace has a large irregular brownish spot on the pars cephalica, a well developed dorsal folium on the abdomen and an elongated white spot in the center of the dark area on the venter.

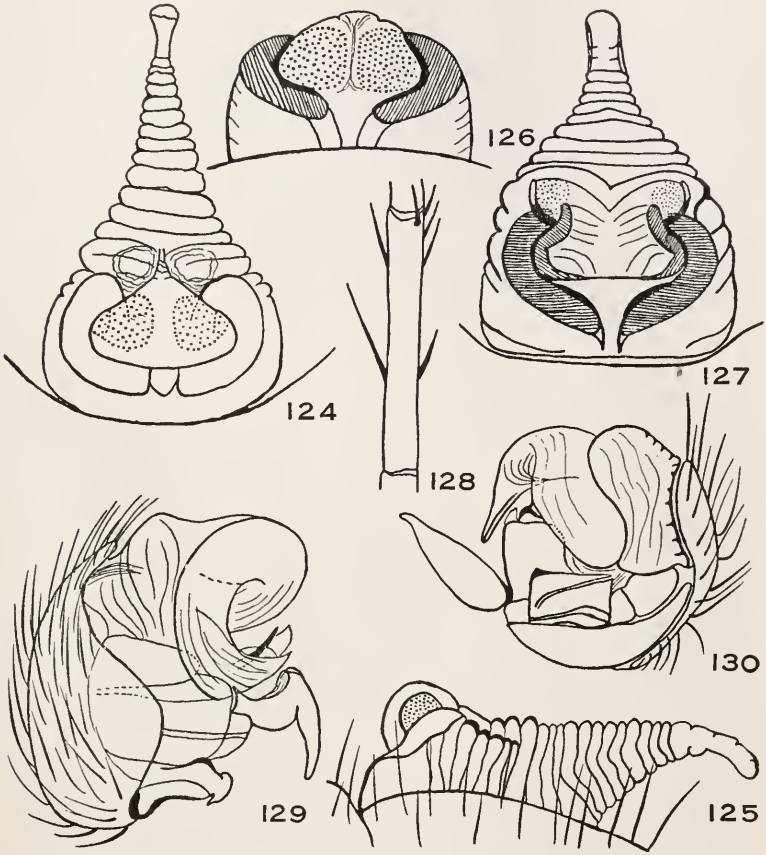
Type locality. The holotype is from Barro Colorado Island, C. Z., July, 1939. Several paratype females have been taken in the same locality as follows: June, 1924 (Banks); June, 1934; June-July, 1936; July-August, 1939; March, 1946 (Schneirla); July-August, 1950.

Eustala semifoliata (O. P. Cambridge)

(Figure 127)

Epeira semifoliata O. P. Cambridge, 1899
Eustala semifoliata F. P. Cambridge, 1904
Eustala semifoliata Petrunkevitch, 1911

Female hypotype. Total length 11.7 mm. There are several distinctive features not sufficiently emphasized in the original or later descriptions. The cephalic part of the carapace is prominently raised; the ME are raised up on a strongly developed ocular cone; the carapace has a heavy coat of white hairs; there is a pair of well developed abdominal shoulder humps; the leg spines are more robust than ordinarily found in females. The ME of the hypotype are defective and, hence, the data on eyes are taken from another specimen. The central ocular quadrangle is wider in front than behind in ratio of 8 : 7, only slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 9 : 6.5 : 8 : 6.5. AME separated from one another by about one and one-half times their diameter, from ALE by four times their



External Anatomy of *Eustala*

Figures 124-126, *E. sedula*
Figure 127, *E. semifoliata*
Figures 128-130, *E. tantula*

Fig. 124. Epigynum from below.
Fig. 125. Epigynum, lateral view.
Fig. 126. Epigynum, a posterior view.
Fig. 127. Epigynum from below.
Fig. 128. Left second tibia from below.
Fig. 129. Male palpal tarsus, lateral view.
Fig. 130. Male palpal tarsus from distal end.

diameter. PME separated from one another by about one and one-half times their diameter, from PLE by about five and one-half times their diameter. Laterals separated from one another by slightly more than their radius. Height of the clypeus equal to two and two-thirds of the diameter of AME. Promargin of the fang groove with four teeth, the fourth the smallest; retromargin with three teeth, all nearly equal in size and fairly robust.

Legs. 1243. Width of first patella at "knee" .7906 mm., tibial index of first leg 12. Width of fourth patella at "knee" .8123 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	5.525	2.470	4.160	4.420	1.625	18.200
2.	5.460	2.340	4.062	4.420	1.625	17.907
3.	3.575	1.430	2.080	2.275	1.235	10.595
4.	5.785	2.405	3.705	4.030	1.430	17.355

Ventral spines on femora as follows: first femur with three on promargin and apparently only one on retromargin near distal end; second femur only one on promargin near distal end; third femur apparently none; fourth femur with one on each margin near distal end.

Epigynum (Fig. 127). With a more or less distinctive pattern of tubules, apertures, and striations; best shown in a figure. The base has not been seen inflated but it probably exists as in *E. bifida.*

Color in alcohol. The general coloring of the two specimens available for study together with the single specimen from the British Museum is quite variable as usual in the genus. Certain features, however, appear to be quite reliable as aids to identification. These are: a pair of dark dots in front of the median thoracic groove; six dark dots in a somewhat procurved transverse row across the anterior end of the thoracic groove; a partial ring of white spots more or less surrounding the bases of the spinnerets; a pair of white spots transversely placed in a black area between the genital groove and base of spinnerets; the whitish sternum is bordered with brown.

Type locality. The female hypotype and another female specimen are from Barro Colorado Island, C. Z., August, 1939 and June, 1936, respectively.

Eustala tantula sp. nov.

(Figures 128-130)

Male holotype. Total length 3.315 mm. Carapace 1.755 mm. long; 1.43 mm. wide opposite intervals between second and third coxae where it is widest; .615 mm. tall and, therefore, about .43 as tall as wide; only gently raised from PME to beginning of steep posterior declivity which passes abruptly to the posterior margin; with a fairly well defined median longitudinal thoracic groove; with two pairs of spinules at anterior end of thoracic groove; with numerous slender spines and spinules in ocular area.

Eyes. Eight in two rows, all dark; LE on moderately prominent tubercles; viewed from above, posterior row moderately recurved; viewed from in front, anterior row straight or slightly procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 18 : 13, wider in front than long in ratio of 12 : 11. Ratio of eyes AME : ALE : PME : PLE = 12 : 8.5 : 9 : 8. AME separated from one another by slightly more than their diameter, from ALE by about two-thirds of their diameter. PME separated from one another by seven-ninths of their diameter, from PLE by about two and one-half times their diameter. Laterals separated from one another by slightly less than the radius of ALE. Height of clypeus equal to the diameter of AME.

Chelicerae. Essentially parallel; with moderately well developed basal boss; basal segment .574 mm. long. Fang groove well defined; promargin with four teeth, retromargin with three small teeth (recorded from a paratype to avoid injury to holotype).

Maxillae. Parallel; convex along retrolateral surface; with a strongly developed serrula; maxillary tooth as usual to oppose ridge on palpal femur.

Lip. Wider than long in ratio of 13 : 9; moderately pointed at distal end; reaches only about two-fifths of the length of the maxillae. Sternal suture gently procurved.

Sternum. Scutiform; as wide as long; a sclerite continues between fourth coxae which are separated by a little more than two-fifths of their width; with numerous long slender spinules

of which the largest eight make a transverse row across the anterior fourth.

Legs. 1243. Width of first patella at "knee" .2383 mm., tibial index of first leg 7. Width of fourth patella at "knee" .2058 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.860	.780	2.535	2.156	.836	9.167
2.	1.950	.572	1.625	1.694	.660	6.501
3.	1.202	.462	.704	.792	.440	3.600
4.	2.015	.585	1.267	1.592	.650	6.109
Palp	.396	.184	.130	——	.594	1.304

First coxa with the usual distal retrolateral ventral hook; dorsal tubercle on first coxa poorly developed. The prolateral groove and ridge on second femur well developed.

Spines. First leg: femur dorsal and prolateral 0-1-1-0-1-1, retrolateral 0-0-0-1-1; ventral 0-2-2-0-2; patella dorsal 1(weak)-1, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 0-1-0-1-0-1-0, prolateral 0-1-0-1-0, retrolateral 0-0-1-0-1-0, ventral 2-0-2(irregular)-0-lr; metatarsus dorsal 0-1-0-1-0-0 prolateral 0, retrolateral 0-1-0-1-0, ventral 0-2-0-0. Second leg: femur dorsal 0-1-1-1-0-1, prolateral apparently 0, retrolateral only one near distal end, ventral three or four along retromargin; patella as in first; tibia dorsal and prolateral as in first, retrolateral 0-1-0-1-1-1, ventral 0-0-lr (Fig. 128); metatarsus appears to be nearly as in first. Third leg: femur dorsal 1-0-1, prolateral and retrolateral only one near distal end, ventral 1-1-0-0-0; patella only dorsal 0-1; tibia dorsal 1-0-1-0, prolateral 0, retrolateral 0-0-1, ventral 0-lp-2; metatarsus dorsal 0-1-0-0, prolateral and retrolateral 0-1-0-0, ventral 0-1-1. Fourth leg: femur dorsal 0-1-0-1, prolateral and retrolateral only one near distal end, ventral 0; patella as in first; tibia dorsal 0-1-0-0-1-0, prolateral 0-1-0-1-0, retrolateral 0-1-1-1-1, ventral 2-0-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1-0, retrolateral 0-1-0-1, ventral 0. Considerable variation of spination has been noted among paratypes and even from left to right in the holotype.

Palp. Complicated; basal femoral tubercle or ridge moderately well developed; patella and tibia short and essentially typical of the genus; the patella has a weak proximal and a long slender

distal spine on the dorsal side as usual. Tarsus: basal tarsal apophysis geniculate near its distal end where the arrow-head is slender; the clavis is moderately robust, deeply excavate at its base where it is broad and strongly geniculate; the uncus is a long slender and somewhat flattened spine; the conductor, largely hidden in ventral view, has a thin transverse process more or less parallel to the uncus and a broad, relatively massive base which is sparsely setose only along a part of its medial border; the massive base of the conductor is only seen well in distal view; the vesicle is very prominent and spirally twisted in a very striking manner; the embolus is apparently hidden by the over-developed vesicle; the terminal laminae have a distinctive pattern the most prominent feature of which is the relatively large quadrilateral body contiguous to the conductor (Figs. 129-130).

Abdomen. Total length 1.852 mm.; longer than wide in ratio of 4 : 3; with numerous long slender dorsal and dorsolateral spinules; other features as usual in the genus.

Color in alcohol. Carapace yellowish with faintly outlined dark dots along base of pars cephalica and a single large dark spot on each side of lateral part of pars cephalica and passing dorsally behind PME. The legs are yellowish with numerous dark spots and rings. The sternum is yellowish with dusky flecks concentrated into dark spots opposite all coxae except the fourth. Abdomen: there is a poorly outlined grayish dorsal folium; on the venter between the genital groove and base of spinnerets there is a light spot containing a dark colored cross the central part of which extends to a narrow dark bar which is a part of a broken ring around the spinnerets and anal tubercle. As usual, no great reliance can be placed upon the color pattern as an aid to identification of the species. The paratypes show many variations in color.

Type locality. The holotype is from Barro Colorado Island, C. Z., August, 1939. Sixteen paratype males have been found from the following localities: Barro Colorado Island, C. Z., July, 1936; Ft. Davis, C. Z., July, 1936; Canal Zone Forest Reserve, C. Z., July and August, 1939; Ft. Sherman, C. Z., August, 1939; Madden Dam Forest, C. Z., August, 1939; near Chiva, C. Z., August, 1950; El Valle, R. P., July, 1936; Boquete, R. P., July, 1939.

Eustala tumida sp. nov.
(Figures 131-132)

Female holotype. Total length 6.045 mm. Carapace 2.73 mm. long, 2.145 mm. wide opposite second coxae where it is widest; 1.04 mm. tall in cephalic region where it is tallest and, therefore, about .48 as tall as wide; with median longitudinal thoracic groove well defined and with a pair of short black spines at its anterior end and another pair of short, light colored spines a little further forward; with a moderately well developed coat of whitish procumbent hair; pars cephalica drawn out into a conspicuous cone upon which both pairs of median eyes are placed in a very distinctive position (Fig. 131).

Eyes. Eight, probably to be considered as being placed in two rows in spite of their unusual position on the cephalic cone, all dark. Viewed from above, posterior row rather strongly recurved; viewed from in front, anterior row strongly procurved. Central ocular quadrangle wider behind than in front in ratio of 39 : 37, wider behind than long in ratio of 39 : 36. Ratio of eyes AME : ALE : PME : PLE = 10 : 8 : 11.5 : 7. AME separated from one another by nearly two diameters, from ALE by 3.7 of their diameter. PME separated from one another by about 1.5 times their diameter, from PLE by about 5.5 times their diameter. Laterals separated from one another by three-fourths of the diameter of ALE. Height of clypeus equal to a little less than four times the diameter of AME.

Chelicerae. Basal segment .88 mm. long. Fang groove as usual with four teeth along promargin and three along retromargin. Other observed features typical of the genus.

Maxillae. Appear to be typical of the genus in all observed features.

Lip. Wider than long in ratio of about 5 : 3; reaches somewhat beyond middle of the maxillae. Sternal suture gently procurved.

Sternum. Scutiform; longer than wide in ratio of about 5 : 4; continued from posterior end by a narrow dark line between fourth coxae which are separated by nearly one-fourth of their width; with low convexities at posterior end and opposite first to third coxae and with a small tuft of bristles and spinules at each convexity; also with a transverse row of long slender spinules between first coxae.

Legs. 1243. Width of first patella at "knee" .3791 mm., tibial index of first leg 9. Width of fourth patella at "knee" .3791 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.185	1.300	2.957	2.665	1.105	11.212
2.	2.925	1.202	2.502	2.502	.975	10.106
3.	1.787	.682	1.040	.975	.650	5.134
4.	2.665	1.250	1.885	2.177	.877	8.854

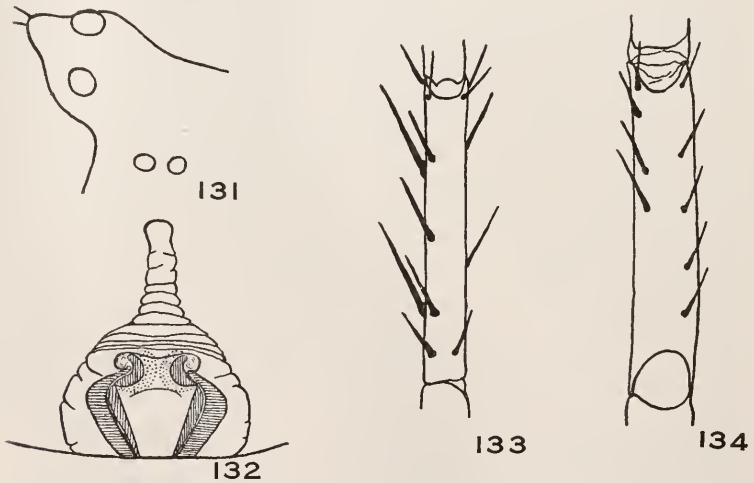
Spines. First leg: femur dorsal 0-1-0-1(weak), prolateral 0-1-1-0-1, retrolateral apparently only one near distal end, ventral 0; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 0-1-1-1-0, prolateral 0-1(weak)-1-1-0, retrolateral the same, ventral 2(irreg.)-lp-0-2; metatarsus dorsal 0-1-1-0-0, prolateral 0-1-0-0, retrolateral 0-1-1-0, ventral 2-2-2-0. Second leg: femur dorsal as in first, prolateral and retrolateral 0-0-0-1-1, ventral 0; patella dorsal and retrolateral as in first, prolateral 0-1-1; tibia dorsal as in first, prolateral 1-1-0-0-1, retrolateral 0-1-1-0, ventral lp-lr-0-lr; metatarsus dorsal and retrolateral as in first, prolateral 0-1-1-0, ventral lr-lr-0-0. Third leg: femur dorsal, prolateral, and retrolateral apparently with only one near distal end in each instance, ventral 0; patella dorsal 1-1, prolateral 0-1-0, retrolateral 0-0-1; tibia dorsal 1-0-0, prolateral and retrolateral 0, ventral 1-1-0-lr; metatarsus dorsal 0-1-0-0-0, prolateral 0, retrolateral 0-1-0, ventral 1-0-1 and many spinules. Fourth leg: femur apparently only one dorsal and one ventral on retromargin both at distal end but a row of retromarginal spinules suggest spines; patella essentially as in third; tibia dorsal 0-1(weak)-0-0-1-0, prolateral 1-1-0-1-1?, retrolateral 1-1-1 (weak), ventral lp-0-2; metatarsus dorsal 0-1-0, prolateral 0-1-1-0, retrolateral 0-1-1-0, ventral 0.

Abdomen. 3.445 mm. long; 2.405 mm. wide about one-fourth from base where is is widest; with a series of five pairs of low dorsolateral tubercles; there is also a low median tubercle about one-fourth from posterior end and another beneath this one and just dorsal to the anal tubercle; the abdomen extends posterior to the spinnerets about one-fourth of its total length; apparently without the long dorsal and dorsolateral abdominal spines so common in the genus but a type of short spines occurs in the

same regions; other observed features appear to be typical of the genus.

Epigynum. This organ illustrates well the difficulties involved in recording the specific epigynal features in the numerous species of *Eustala* and in making these distinctions clear to other workers. Here the apertures are about two diameters apart; the central part of the base exhibits a characteristic shape best shown by a figure; the scape is of moderate length and springs quite abruptly from the base (Fig. 132). The base in the holotype is not sufficiently extended to make practicable a drawing from a lateral aspect.

Color in alcohol. Carapace: yellowish with small irregular reddish brown spots over the dorsal part; in the region of the clypeus there are irregular small gray spots; at the base of the pars cephalica there is a white triangular subchitinous spot with



External Anatomy of *Eustala*
Figures 131-132, *E. tumida*
Figures 133-134, *E. vegeta*

Fig. 131. Cephalic cone, lateral view.
Fig. 132. Epigynum from below.
Fig. 133. Left second tibia from below.
Fig. 134. Right fourth femur from below.

its apex directed posteriorly. The sternum is nearly white with irregular chalk-white subchitinous marginal spots. The legs are yellowish with grayish spots, rings, and bars. Abdomen: the dorsal folium is poorly outlined by remnants only; the whole dorsal and dorsolateral areas are largely white from a multitude of white subchitinous granules but there are numerous reddish dots and streaks as well as many black dots and streaks; on the venter there is an irregular white spot, composed of many subchitinous granules, just in front of the spinnerets and another similar spot between that and the genital groove and on each side of the latter there is a large irregular elongated dark gray spot.

Type locality. The holotype is from Summit, C. Z., August, 1950.

Eustala vegeta (Keyserling)

(Figures 133-138)

Epeira vegeta Keyserling, 1865
E. vegeta Keyserling, 1892
Acacesia vegeta Simon, 1895
Eustala vegeta F. P. Cambridge, 1904
E. vegeta Petrunkevitch, 1911

In defining the species, F. P. Cambridge emphasized the following features of the male palp: the uncus is without the strong transverse enlargement at the base characteristic of *E. bifida;* it does not have the enlarged shoulder on the inner margin of the uncus as in *E. guttata;* the embolus is shorter than in *E. scutigera;* the conductor is not sharply angled as in *E. scutigera.* F. P. Cambridge also stressed the following features in the epigynum: the scape is "abruptly narrowed at its apex" but it is broad and transversely wrinkled at the base; the apertures, "marked by circular black spots" are two to three diameters apart. In view of the large number of species and the difficulty of separating those which are closely related these vague and very general definitions leave us with much uncertainty. The study of specimens on loan from the British Museum has greatly helped in clarifying the distinctions between this and related species so that I feel fairly confident of the facts as stated below.

Male hypotype. Total length 4.452 mm. With the typical form of the body. Central ocular quadrangle wider in front than behind in ratio of 35 : 26, wider in front than long in ratio of 35 : 32. Ratio of eyes AME : ALE : PME : PLE = 11 : 8 : 9 : 8. AME separated from one another by nearly 1.5 times their diameter, from ALE by the same distance. PME separated from one another by about five-fourths of their diameter, from PLE by slightly more than three times their diameter. Lateral eyes separated from one another by their radius. Height of clypeus equal to the diameter of AME. Secondary sexual characters on first coxae, maxillae, and second femora typical of the genus.

Legs. 1243. Width of first patella at "knee" .3249 mm., tibial index of first leg 9. Width of fourth patella at "knee" .2708 mm., tibial index of fourth leg 10.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	3.120	1.072	2.567	2.372	1.040	10.171
2.	2.470	.965	1.755	2.015	.942	8.147
3.	1.495	.585	.910	.900	.565	4.455
4.	2.210	.910	1.690	1.852	.812	7.474
Palp	.430	.264	.154	——	.880	1.728

The first femur appears to have only two ventral spines, one on each margin near distal end; the second femur has three ventral spines along the retromargin and one near distal end on the promargin; the third femur appears to have three ventral spines along the promargin and none on the retromargin; the right fourth femur has five along the promargin and four along the retromargin (Fig. 134), while the left femur has fewer. The second tibia has special spines as shown in Figure 133.

Palp. Maxillary tooth, femoral ridge, and patellae typical of the genus; the dorsal lobe of the tibia is somewhat longer than in most species. Tarsus: the basal tarsal apophysis is a typical arrow head with only slight distortion except the usual bend in the shank; the clavis is moderately robust and has a shallow basal ventral concavity which is very setose; the uncus is a distinct hook with its curvature toward the tip of the embolus as shown in F. P. Cambridge's Figure 16; the conductor is fairly large, has no lobe such as that found in the palp of *E. scutigera* but has a depression within which the uncus lies and

it also has a deep dorsolateral concavity; the embolus is of moderate length, slender, gently curved; the terminal laminae are raised into a high prominence contiguous to the conductor and have a prominent tubercle dorsal to the prominence (Figs. 135-136).

Female hypotype. Total length 7.02 mm. Body form like that of male.

Legs. 1243. Width of first patella at "knee" .4007 mm., tibial index of first leg 11. Width of fourth patella at "knee" .3574 mm., tibial index of fourth leg 13.

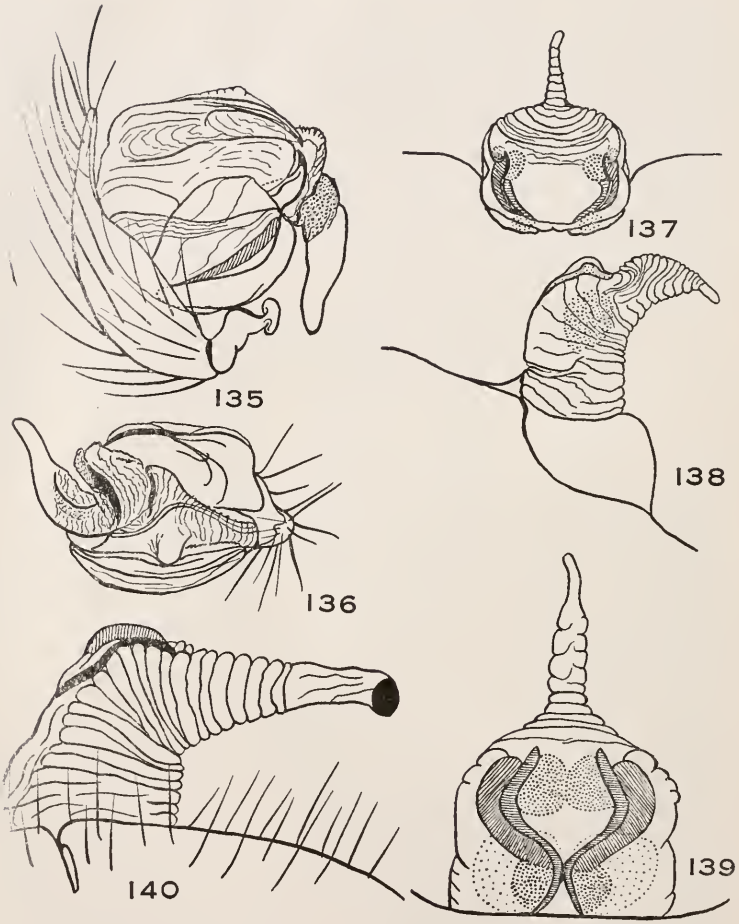
	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	3.120	1.170	2.535	2.210	1.105	10.140
2.	2.730	1.170	2.112	1.950	1.040	9.002
3.	1.690	.747	.910	1.007	.715	5.069
4.	2.632	1.040	1.625	1.885	.910	8.092

First femur with a single ventral spine on both margins but apparently none of the other femora has ventral spines.

Epigynum (Figs. 137-138). Much like that of *E. scutigera;* the scape is relatively longer and it arises more abruptly than in that species; both apertures and spermathecae are much farther apart than in *E. scutigera.*

Color in alcohol. The color is much the same as in *E. scutigera.* The two rows of dots on the carapace show well in the male but are faint in the female; this color feature appears to be less consistent than in several other species. In both hypotypes the sternum is yellowish with a fairly broad brownish margin. The legs have the common yellowish color with many brownish dots, bars, and rings; in the male hypotype the femora are nearly all brown except the yellowish proximal third. The dorsal folium is clear and definite on the abdomen of the male and less well outlined in the female. In both the venter has a dark and more or less quadrilateral area between the genital groove and the base of the spinnerets containing the usual white spot, small and rounded in the male but larger and elongated in the female.

Collection records. The male hypotype is from Tlacotalpan, Veracruz, Mexico, July, 1946 (H. Wagner); the female hypotype is from Vera Cruz, La Planta Moctezuma, near Fortin, Mexico, July, 1947 (C. and M. Goodnight). Other females are



External Anatomy of *Eustala*
Figures 135-138, *E. vegeta*
Figures 139-140, *E. venusta*

Fig. 135. Male palpal tarsus, lateral view.
Fig. 136. Male palpal tarsus, distal view.
Fig. 137. Epigynum from below.
Fig. 138. Epigynum, lateral view.
Fig. 139. Epigynum from below.
Fig. 140. Epigynum, lateral view.

from the same localities as those from which the hypotypes were taken, and other parts of Mexico as follows: Cordova, Jalapa, Veragua, 1946 (J. C. and D. L. Pallister); Tlapocayan, Veragua, July, 1946 (H. Wagner); Mantla, Veragua, July, 1946 (H. Wagner). Males are in my collection from: Costa Rica, Santa Maria (Tristan), no date; Porto Bello, R. P., August, 1936.

Eustala venusta sp. nov.

(Figures 139-140)

Female holotype. With the conventional round-triangular form. Total length 7.67 mm. Carapace 3.25 mm. long; 2.697 mm. wide opposite interval between second and third coxae where it is widest; 1.365 mm. tall and, therefore, about .5 at tall as wide; median thoracic groove deep and well defined; with numerous short spinules and a fairly well developed coat of whitish procumbent hair over most of the surface.

Eyes. Eight in two rows, all dark; viewed from above, posterior row strongly recurved; viewed from in front, anterior row gently procurved, measured by centers; central ocular quadrangle wider in front than behind in ratio of 37 : 34, only slightly wider in front than long. Ratio of eyes AME : ALE : PME : PLE = 10 : 8.5 : 11 : 9. AME separated from one another by slightly more than twice their diameter, from ALE by four times their diameter. PME separated from one another by nearly one and one-fourth times their diameter, from PLE by nearly 4.6 times their diameter. Laterals separated from one another by two-thirds the diameter of PLE. Height of clypeus equal to 6/5 of the diameter of AME.

Chelicerae. Basal segment 1.3 mm. long; general features as usual in the genus. Fang groove finely dentate; promargin with four teeth, as usual with second and fourth smaller; retromargin with three teeth.

Maxillae. Appear to be completely typical of the genus in all observed features.

Lip. Wider than long in ratio of 4 : 3; reaches to about the middle of the maxillae. Sternal suture distinctly procurved with anterolateral corners of the sternum distinctly tuberculous.

Sternum. Scutiform; longer than wide in ratio of 62 : 55;

truncated at posterior end which is not continued between fourth coxae which are separated from one another by about one-sixth of their width; deeply scallopped marginally opposite all coxae except the first; only moderately convex opposite first to third coxae; well supplied with stiff spinules.

Legs. 1243. Width of first patella at "knee" .5307 mm., tibial index of first leg 9. Width of fourth patella at "knee" .5198 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.875	1.722	3.900	3.185	1.235	14.917
2.	4.160	1.560	3.120	2.827	1.170	12.837
3.	2.405	.858	1.210	1.232	.758	6.463
4.	3.835	1.560	2.405	2.550	.975	11.325

Spines. First leg: femur dorsal 0-0-1-0-1-1, prolateral 0-0-1-1-1-1, retrolateral 0-0-0-1-1-1, ventral 0; patella dorsal 1(weak)-1, prolateral and retrolateral 0-1-1-0; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-lr-lp-lr-lp-lp-2; metatarsus dorsal and prolateral 0-1-0-1-0-0, retrolateral 0-1-0-1-0, ventral 2-2-0-lp. Second leg: femur dorsal, retrolateral, and ventral as in first, prolateral 0-0-1-1-1; patella as in first; tibia dorsal as in first, prolateral and retrolateral 0-1-0-1-1, ventral 2-2-2-2; metatarsus dorsal 0-1-0-1-0-0, prolateral and retrolateral 0-1-0-1-0, ventral 2-lr-0-lp. Third leg: femur dorsal 0-1-1-1, prolateral and retrolateral 0-0-0-1-1, ventral 0; patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-0-1, prolateral 0-1-0-1, retrolateral 0-0-1, ventral lp-lp-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1, retrolateral 0-1-0, ventral lp-lp-1-1. Fourth leg: femur dorsal 0-1-0-1-1, prolateral 0-0-0-1-1, retrolateral only one near distal end, ventral 0; patella as in third; tibia dorsal 1-0-1-1-0, prolateral 1-1-1-1, retrolateral 0-1-1, ventral lp-lp-lp-2; metatarsus dorsal 0-1-0-1-0-0, prolateral 0-1-1-1, retrolateral 0, ventral lp-lp-lp-lp. Palp: femur with dorsal spines 0-1-1; patella with dorsal spines 1-1, prolateral 1-0; tibia with dorsal spines 0-1-0, prolateral 1-1, retrolateral 0-1; tarsus with many spines and spinules irregularly distributed. Palpal claw pectinate in a single row of nine or ten slender teeth.

Abdomen. 5.135 mm. long; widest about one-fifth from base where convexities suggest suppressed shoulder humps. Other observed features are typical of the genus.

Epigynum. Base with nearly the usual conventional forms of tubules, striations, apertures; spermathecae large and clearly defined; scape relatively long and arises from base abruptly, and slender throughout as shown by lateral views (Figs. 139-140).

Color in alcohol. Carapace yellowish with faint darker striations contiguous to cephalic groove; there is a brownish dot on each side of median thoracic groove opposite its middle and another faint dot on each side in front of the groove. Sternum yellowish with a broad broken brownish margin. Legs: yellowish with many brown bands. Abdomen: the dorsal folium is fairly well outlined in the holotype but is highly variable in the paratypes; the venter has a large brown quadrilateral area between the genital groove and the base of the spinnerets containing an elongated white spot which seems to be quite persistent among the paratypes.

Type locality. The female holotype is from Barro Colorado Island, C. Z., July, 1950. About 25 female paratypes from the following localities have been studied: Barro Colorado Island, C. Z., June-July, 1934; July-August, 1936; July-August, 1939; June-August, 1950. Canal Zone Forest Reserve, C. Z., August, 1939. Near Chiva, C. Z., July, 1950. Summit, C. Z., July-August, 1950.

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